The Journal of ARACHNOLOGY

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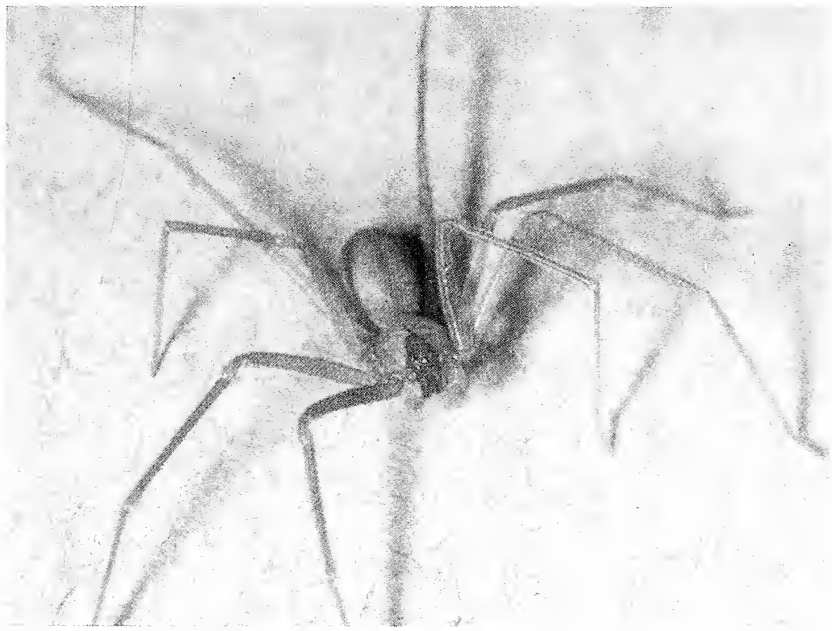

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BEHAVIOR OF WEB-INVADING SPIDERS *ARGYRODES ARGENTATUS* (THERIDIIDAE) IN *ARGIOPE APPENSA* (ARANEIDAE) HOST WEBS IN GUAM

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ABSTRACT. Most *Argyrodes* live in the webs of other spiders, stealing food from the host, scavenging small prey from the web or killing and eating the host. I observed the behavior of *A. argentatus* from Guam, where it is a frequent inhabitant of the large orb webs of *Argiope appensa*. I examined the proportion of time spent in different activities, whether behavior differed between the sexes and if population density of *Argyrodes* on a host web affects *Argyrodes* behavior. *Argyrodes* spent 55% of the time hanging immobile and inverted in the support strands at the webs' margin. This was significantly more time than that spent in stationary activity, forward movement at the web's margin, feeding, foraging on the sticky spiral or in aggressive interaction. Females foraged significantly more often than did males, though the sexes spent about the same amount of time feeding and in other activities. Females also engaged in more bouts of feeding and 21% of these bouts were at prey bundles prepared by the host. In contrast, males invariably foraged for small insects unnoticed by the host.

Keywords: Kleptoparasite, Mariana Islands, Micronesia, Araneae

Most members of the large, cosmopolitan genus of *Argyrodes* Simon 1864 live in the webs of other spiders. They feed on small insects that have gone unnoticed by the host (Whitehouse 1986), prey stolen from the host (Robinson & Olazarri 1971), the host itself (Trail 1980; Tanaka 1984; Larcher & Wise 1985) or host-web silk (Shinkai 1988; Tso & Severinghaus 1998). *Argyrodes* may also capture prey themselves using an abandoned host web (Larcher & Wise 1985) or use their own small web (Whitehouse 1986).

Despite a growing literature on the ecology of this interesting spider genus (e.g., Henaut 2000; Miyashita 2001, 2002) and the prospect of powerful comparative phylogenetic approaches (Agnarsson 2002; Whitehouse et al. 2002), the behavior of most species is still poorly known. One little studied species is *Argyrodes argentatus* O.P. Cambridge 1880, a small (adult female body length c. 5 mm) spider with a tall, conical, silvered abdomen that is reported from Madagascar eastward through southeast Asia to South America (Cambridge 1880; Exline & Levi 1962; photo in Koh 2000). General observations of this species have been made on host webs of *Argiope argentata* (Fabricius 1775) in Panama (Robinson & Olazarri 1971) and *Nephila maculata* (Fabricius 1793) from New Guinea (Robinson & Robinson 1973). *Argyrodes argentatus* on the island of Guam in western Micronesia is a frequent inhabitant of the large orb webs of several species. Kerr and Quenga (2003) report on population variation in different host species and habitats for Guamanian *Argyrodes*, including *A. argentatus*. The most common orb-weaving spider on Guam hosting *A. argentatus* in their webs is *Argiope appensa* (Walckenaer 1841) (Araneidae) (25 mm), which occurs from New Caledonia and across the tropical western Pacific to Hawaii (Levi 1983). It builds a nearly vertical planar orb web with sticky spiral strands, occasionally with cruciate or diagonal strips of white silk near the center (Kerr 1993). In this paper, I record further aspects of the behavior of *Argyrodes argentatus* from Guam. Specifically, I asked: (1) What is the proportion of time spent in different activities? (2) How does behavior differ between the sexes? (3) Does population density on a host web affect *Argyrodes* behavior?

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METHODS

Surveys.—The surveys were performed in Mangilao and Ukudu (Dededo), Guam, 6–31 August 1989 in native forest, beach strand or disturbed vegetation. Guam (13° N, 145° E; 540 km^2) is a volcanic and tectonically uplifted limestone arc island in the western Pacific Ocean. Voucher specimens of *Argyrodes argentatus* (adult males and females) and its host *Argiope appensa* (adult females) are deposited at the Department of Zoology, Southern Illinois University at Carbondale and the University of Guam Herbarium. Censusing of haphazardly encountered webs was conducted during periods of no rain between 0900–2100 h, since a preliminary survey (A. Kerr pers. obs.) suggested that the spiders were most active during this time. A dim red light was used during nocturnal observations to avoid disturbing the spiders or attracting insects to the host web. The density of *Argyrodes* was measured as number of spiders per unit area of host web. The area of *Argiope* host webs, as defined by the outermost spiral strands, was computed as an ellipse based on horizontal and vertical web diameters. To determine the behavior of *Argyrodes*, I recorded for 20 *Argiope appensa* host webs the activities of each *Argyrodes* found, after which the web was no longer used. In these webs, a total of forty-eight *Argyrodes argentatus* (23 females, 21 males and 4 juveniles) were each observed repeatedly for ca. 15 s at 5-min intervals (sensu Vollrath 1976) over a period of 1.5–4 h per web for a total of 1,286 separate observations in 107.2 spider hours. These same host webs and spiders, and their recorded behaviors, were used in all analyses. Twelve webs (60%) were from beach-strand vegetation, six (30%) were from disturbed vegetation and two (10%) occurred in native forest. I categorized behavior as quiescence (immobile and inverted), foraging (moving forward on prey-catching spiral while rotating leg pair I sensu Whitehouse 1986), forward movement on other silks at the web's margin, feeding (contact between mouthparts and prey), stationary activity (grooming, modifying silk, mating), or as agonism-avoidance (rushing towards or retreating from other spiders).

Statistical analyses.—The proportion of time a spider spent performing an activity was computed as the number of observations for that activity divided by the total number of observations on that spider. Intersexual differences in time spent in a behavior were examined with one-way anovas or Kruskal-Wallis procedures. I examined the relationship between the density of *Argyrodes argentatus* and behavior using simple linear regressions. Recently hatched spiderlings were sometimes extremely numerous on a web, but such aggregations dispersed quickly. To prevent them from inflating estimates of population density on webs, spiderlings were excluded from the analyses. To meet assumptions of parametric procedures, densities of adult *Argyrodes* were square-root or log transformed and proportions were arc-sine-square root transformed when necessary. Statistical outliers were detected using Dixon's tests (Sokal & Rohlf 1981). Tests of association with categorical variables were done with a G test with Williams' correction for small sample size. Then homogeneity of variances was checked with Bartlett's tests and normality confirmed with Rankit plots (Sokal & Rohlf 1981). Otherwise analogous nonparametric procedures were used.

RESULTS

General observations.—*Argyrodes argentatus* would sometimes glean small insects from the host web. These were sometimes eaten where found or wrapped and taken to the margin of the host web and eaten there. *Argyrodes* would also remove and eat spiral catching silk from a host web, sometimes removing large sections. The host *Argiope appensa* would sometimes leave wrapped small prey at the capture site. These prey bundles were sometimes removed by *Argyrodes argentatus*, who would cut them from the web and hoist them to the host web's barrier strands. At other times, *A. argentatus* would feed together on prey bundles held in the host's mouth as the host rested at the web's hub. I also observed one possible instance of predation on the host by *A. argentatus*. In this case, several *A. argentatus* were feeding at the web hub on a dead adult female *Argiope appensa* host that had been alive the previous day.

Proportion of time in activities.—Proportional time differed significantly between activities via a Kruskal-Wallis procedure (H = 121.62, $P < 0.001$). The 48 *Argyrodes* (fe-

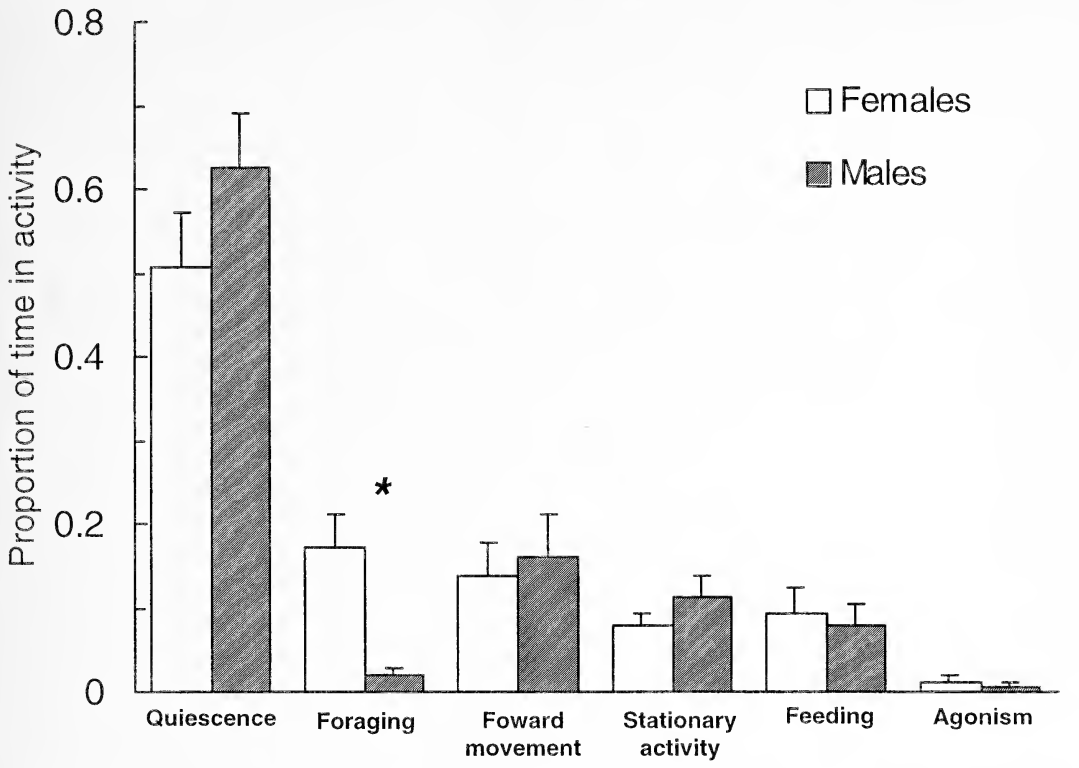

Figure 1.—Time budget of adult male and female *Argyrodes argentatus*. Males denoted by striped bars. Asterisk indicates a significant difference via a one-way anova.

males, males and juveniles combined) in the 20 host webs spent significantly more time hanging immobile and inverted in the support strands at the webs' margin than in stationary activity, forward movement at the web's margin, foraging, feeding or agonism (minimum pairwise $G = 11.02$, $P < 0.001$ adjusted for multiple comparisons). Other activities on average occupied no more than 9% of the time. Instances of agonism were least frequent, occurring 0.7% of the time.

Sex related differences.—When sexes were considered separately, there was one notable significant difference in behavior. Females foraged significantly more often than did males (females: mean proportion ± 1 SE = 0.172 ± 0.039; males: 0.019 ± 0.010; $F_{1,42} = 19.776$, $P < 0.001$) (Fig. 1). Other behaviors were not significantly different ($P > 0.05$) between the sexes: quiescence (females: 0.506 ± 0.066; males: 0.625 ± 0.065; $H = 0.798$, $P = 0.372$), stationary activities (females: 0.079 ± 0.014; males: 0.113 ± 0.026; $H = 2.19$, $P = 0.138$), movement on support strands (females: 0.138 ± 0.039; males: 0.160 ± 0.010; $H = 1.57$, $P = 0.210$), or agonism (females: 0.011 ± 0.010; males: 0.005 ± 0.005; $H = 0.89$, $P = 0.344$). Of the 50 bouts of feeding (continuous feeding through multiple observations), 38 were by females and 12 were by males. Females more often fed on large prey bundles prepared by the host (21% of feeding events) than did males, who were never observed feeding on prey bundles, but rather fed on small prey (tiny dipterans and homopterans) caught on the spiral strands, but unnoticed by the host. This intersexual differences in type of prey used was not significant ($G_{adj} = 3.01$; $P = 0.0829$).

Effects of density.—The density of *A. argentatus* on host webs varied by about an order of magnitude, from a minimum of 0.027/100 cm² to 0.26/100 cm² or 1–8 individuals per web. The proportion of time that adult *A. argentatus* spent feeding on prey was weakly but significantly and inversely related with the density of this species on *Argiope* webs ($n = 44$; $P = 0.0462$; $r^2 = 0.142$; $y = -0.776 x + 0.430$) (Fig. 2). I observed only six instances of agonism between *Argyrodes* individuals or

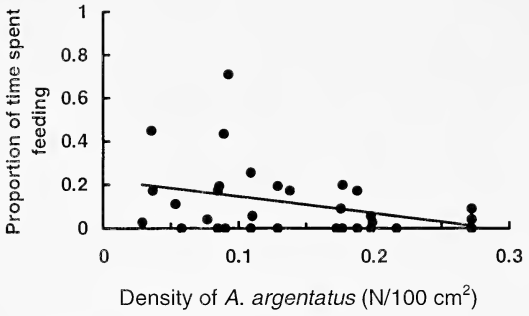

Figure 2.—Proportion of time spent feeding by adult *Argyrodes argentatus* versus its population density on host webs of *Argiope appensa*.

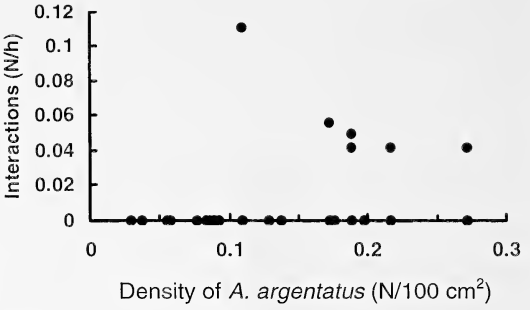

Figure 3.—The rate of agonism and avoidance of hosts and other *Argyrodes* versus adult *Argyrodes argentatus* population density on host webs of *Argiope appensa*.

between *Argyrodes* and their host. In three of these encounters, the aggression resulted in one of the pair of *Argyrodes* leaving the web. Pooled intra-*Argyrodes* and *Argyrodes*-host agonism was not significantly correlated with *Argyrodes* density ($r^2 = 0.005$; $n = 44$; $P > 0.05$) (Fig. 3). Other behaviors were also not significantly correlated with the density of adult *A. argentatus*: quiescence ($r^2 = 0.009$), stationary activities ($r^2 = 0.051$), movement on support strands ($r^2 = 0.051$), or foraging ($r^2 = -0.021$).

DISCUSSION

Of the *Argyrodes* species that take food in the webs of larger spiders, sometimes foraging is for small prey unnoticed by the host (Whitehouse 1986; Pasquet et al. 1997), while at other times *Argyrodes* concentrates on sharing large prey captured by the host (Vollrath 1979; Whitehouse 1997). There may also be species-specific differences in the use of these strategies (Tso & Severinghaus 2000). Intersexual differences in foraging mode have also been noted. Cangialosi (1990) found that male *Argyrodes ululans* O.P. Cambridge 1880 in webs of *Anelosimus eximius* (Keyserling 1884) spend more time foraging than do females. This is apparently because females wait until alerted by the hosts to steal freshly captured prey, while males more often search for previously caught prey for which it presumably spends more time in locating. Conversely, in this study, female *A. argentatus* spent more time foraging than males. I also did not find an intersexual difference in proportional feeding times (Fig. 1) (contra Cangialosi 1990). However, females engaged in over three times as many bouts of feeding as did males (38 versus 12, respectively). Hence feeding in females is spent in more, but shorter feedings. This difference might occur if some of the feeding events by females were shorter because of higher food quality. Females spent 21% of feeding events at large prey bundles, while males were never observed doing so. One possibility that might account for these differences between the sexes is if females possess a larger energy and nutrient budget, such as needed for egg development and egg-sac construction (Toft 1999).

Food availability can affect a spider's growth rate, adult size, fecundity (Miyashita 1990, 1991) and web-site tenacity (Caraco & Gillespie 1986; but see Smallwood 1993), as well as influence the degree of intra- and interspecific competition (Spiller 1984). *Argyrodes antipodianus* are known to aggressively compete for food (Whitehouse 1997), suggesting that food is a limiting resource. In this study, the time adult *Argyrodes argentatus* spent feeding was inversely proportional to their density on host webs (Fig. 2). One possible explanation for this pattern is that as *Argyrodes* density increases, so does competition for food because of increased intraspecific agonism among *Argyrodes* and aggression by hosts which limits access to food. However, aggressive interactions were very few and uncorrelated with *Argyrodes* density (Fig. 3). Another possibility is that time spent feeding is positively correlated with an unmeasured variable, such as food quality, which itself negatively correlates with *Argyrodes* density. Webs may be densely populated with *Argyrodes* because of better food

that requires less time to consume. For example, feeding bouts (defined as a putatively continuous term of feeding through consecutive observations made five minutes apart) are shorter when feeding with the host on large predigested prey bundles. This has also been observed by Whitehouse (1997) in another species, *A. antipodianus* O.P. Cambridge, 1880.

There is growing interest in the evolution of behavior in *Argyrodes* (Whitehouse et al. 2002). Several researchers are generating a phylogeny of the genus to use, for example, in ancestral state analyses of the correlated evolution of kleptoparasitism and araneophagy. The success of this promising approach will depend not only on the quality of the phylogenetic estimates, but also in large measure on natural history information from a behaviorally diverse suite of *Argyrodes*. Robinson and Olazarri (1971) listed several observations on the behavior of *A. argentatus* in *Argiope argentatus* host webs from Panama. Most of the behaviors of Panamanian *Argyrodes* appeared to parallel those of populations in *Argiope appensa* host webs from Guam in the western Pacific. Guamanian populations also gleaned insects from the host web, stole host food bundles, fed with the host and appeared to occasionally attack, kill and feed on the host. However, I did not find, as reported for Panamanian populations, that *Argyrodes* removed host-wrapped prey bundles from the host web. Despite this possible difference, there is apparently little intraspecific variation in these behaviors within the nearly pantropical species *A. argentatus*.

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SCYTODES VS. *SCHIZOCOSA*: PREDATORY TECHNIQUES AND THEIR MORPHOLOGICAL CORRELATES

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ABSTRACT. Wolf spiders (Lycosidae) typically subdue prey using their legs for capture and their fangs for the injection of venom. Spitting spiders (Scytodidae), in contrast, subdue prey by entangling them, at a distance, in a spitted mixture of silk, glue, and venom that immobilizes and may also kill them. We selected individuals of *Schizocosa duplex* (Lycosidae) and *Scytodes* sp. (Scytodidae) of approximately the same mass and carapace width to provide a quantitative assessment of their relative allocations of biomass to morphological features that might be expected to vary with prey-capture technique. As expected, the wolf spiders allocated significantly more to legs, chelicerae, and fangs, and significantly less to the venom glands, than did the spitting spiders. Further comparisons of the legs and chelicerae of the two species provided surprises. First, the legs of *Scytodes* were 42% longer than those of *Schizocosa* despite smaller overall allocation to the legs in *Scytodes*. And second, although the relative sizes of the chelicerae differ greatly, the shapes of the chelicerae of *Schizocosa* and *Scytodes* were not significantly different despite the radically different tasks those structures must fulfill.

Keywords: Spitting spider, wolf spider, resource allocation, allometry

Spitting spiders (Araneae, Scytodidae) are renowned for their eponymous method of subduing prey and, at least occasionally, deterring predators (Gilbert & Rayor 1985; Jackson & Pollard 2001). They eject a glutinous mixture of silk, adhesive, and toxin, all from their enlarged venom glands (Monterosso 1928; Millot 1929, 1930; Bristowe 1931; Dabelow 1958; MacAlister 1960; Kovoor 1987; Foelix 1996), that rapidly immobilizes the insects and spiders that typically constitute their diet (Nentwig 1985).

What distinguishes this peculiar way of subduing prey from other methods used by spiders is not the use of glue-adorned fibers. Such a combination of materials typifies the prey capture spirals of araneid orb-weavers (e.g., Peters 1987; Foelix 1996; Opell 1997) and the webs of other spiders that produce sticky silk from their opisthosomal spinnerets. Rather, the uniqueness of the method is attributable both to the prosomal source of the materials, the venom glands (Kovoor 1987; Kovoor & Zylberberg 1972), and to the forceful and directed ejection of the mixture (Millot 1930; Bristowe 1931).

Our interest in spitting spiders began with a quest to quantify their expectorant capabilities, but quickly turned to the suite of morphological characteristics that, together, appear to contribute to the overall effectiveness of spitting as a predatory method. These characteristics include (a) venom glands large enough to secrete and store quantities of silk, glue and venom sufficient for multiple predation attempts, (b) ducts and nozzles large enough to accommodate rapid flows of glutinous material and (c) sensory structures capable of conveying adequately accurate targeting information. We know from earlier work that scytodid spiders have disproportionately large venom glands (e.g. Millot 1929), that the secretory epithelia of these glands extend into the chelicerae (Kovoor & Zylberberg 1972), and that the orifice through which the spit is ejected is located near the base of the fang (Kovoor & Zylberberg 1972) rather than at its usual location near the fang's distal end (Foelix 1996). We also know that these spiders are primarily nocturnal hunters that appear to use their legs in sensory exploration of their environment, detecting prey via either vibrations or viadirect tactile sensations (Nentwig 1985). The structure and orientations of their eyes, then, may be of little

consequence for the triggering and the accuracy of their spitting, but the structure of the legs may be crucial.

To assess quantitatively the morphological correlates of the predatory specialization seen in spitting spiders, we compared *Scytodes thoracica* (Latreille 1802) and *S. fusca* Walckenaer 1837 with a comparable sized wolf spider, *Schizocosa duplex* Chamberlin 1925 (Araneae, Lycosidae). Like scytodids, the wolf spiders are often nocturnal hunters that generally do not use webs in prey capture. Unlike the spitting spiders, however, the wolf spiders lunge and grab prey with their legs and bite the prey immediately. We knew at the outset that these differences in predatory technique are strongly reflected in the directly supporting morphology–the wolf spider's legs, chelicerae, and fangs are more robust than those of the spitting spider, and the spitting spider's venom glands are substantially larger than those of the wolf spider (Monterosso 1928; Millot 1929, 1930; Foelix 1996)–although those specific comparisons have not previously been made in the literature.

These differences, we assumed, also reflect a history of selective pressures that have modified the allocation of resources (Huxley 1932; Calder 1984) within developing spiders. For example, physiological and metabolic resources that could have been devoted to the production of eggs in an adult female wolf spider are, instead, devoted to the production and maintenance of stout legs and chelicerae. Our adaptionist assumption was that the differences we would detect between these two kinds of spiders mark differences in natural selection that moved each lineage toward an optimal allocation of physiological resources. At the same time, we recognized that the very disparate lineages of the lycosids and the scytodids could contribute substantively to the differences we would detect. For example, the upright, cursorial habit of wolf spiders differs fundamently from the usually supine, sedentary habit of spitting spiders, and the consequent disparity in morphology need not be directly related to differences in predatory techniques.

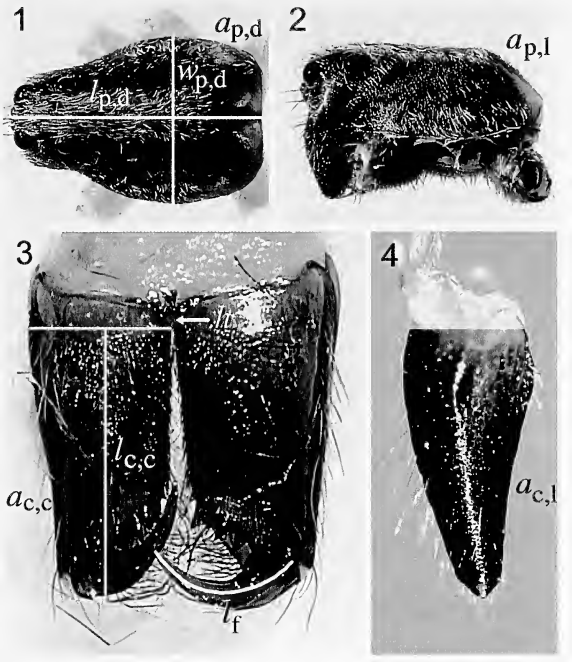
METHODS

Spiders.—We used 12 adults (8 females, and 4 males) of the wolf spider, *Schizocosa duplex*, drawn from the collection of P. Miller and G. Stratton, maintained in 80% alcohol, at the Department of Biology, University of Mississippi. All were originally collected in Mississippi (MS., Panola County, nr Sardis Dam, Sandstone Nature Trail 34° 23.616 N, 89° 47.496 W., 5 May 2002). Our specimens of the spitting spiders were provided, live, by James Carrel and Hank Guarisco (9 adult female *S. thoracica*) from Florida (Fl., Highlands County, 10 km S. of Lake Placid, Archbold Biological Station; FL, Santa Rosa County, Pensacola), and by Gerald Baker (1 adult female *S. fusca*) from Mississippi (MS., Oktibbeha County, in Starkville). Subsequent to their use in biomechanics studies, the spitting spiders were preserved in 80% alcohol until we used them in this study. We have deposited voucher specimens in the Mississippi Entomological Museum.

Our use of both sexes in the wolf spider species *S. duplex* and of two species in the spitting spider genus *Scytodes* could, in theory, have complicated our analyses and skewed our results. Most spider species are sexually dimorphic, and this is the case even among the Lycosidae (Walker & Rypstra 2001, 2002) in which the dimorphism is less striking than in many other families of spiders (Foelix 1996). Similarly, species within the same genus can differ both in overall size and in the relative sizes of individual parts. These differences notwithstanding, we pooled the two wolf spider sexes and pooled the two spitting spider species, electing to increase our sample size despite the small expected increase in variance that might result from the pooling.

Morphometry.—Spiders preserved in alcohol lose mass due to evaporation when exposed to air. To minimize the consequent inaccuracies, we weighed the spiders and their parts, to the nearest 0.1 mg, during < 2 min exposure to air after initially removing surface moisture by blotting with dry filter paper. Because very small objects, such as the chelicerae and venom glands, are especially susceptible to rapid drying and thus to spurious mass measurements, we also made digital images of the structures in which we were interested.

In one series of images, we devoted a single frame (6.1 MP, Nikon D100) to an entire but dismembered spider. These images showed dorsal views of the separated prosoma and opisthosoma and lateral views of the legs and



Figures 1–4.—Image-derived morphometry methods illustrated for *Schizocosa duplex*. Lengths, widths, and areas are represented by their italic initials. The first subscript represents the structure (e.g., prosoma, chelicera, fang) and the second subscript designates the view (e.g., dorsal, lateral, caudal). The position of the horizontal line (3), which delimited one end of $l_{c,c}$, was determined by the location of the bottom margin of the hinge (h) around which the jaws rotate. Volumes were calculated as described in the text.

pedipalps. In another series of images collected via dissecting microscope (Olympus SZX12) and dedicated digital camera (Olympus 750), we devoted a single frame (0.32 MP) each to dorsal, lateral and frontal views of the prosoma (including chelicerae), caudal and lateral views of the chelicerae (after detachment from the prosoma), and dorsal and lateral views of the venom glands. We measured lengths, widths, and areas of the structures in these images using NIH Image (NIH shareware) and MetaMorph (Universal Imaging Corporation).

We used a scanning electron microscope (Amray 1200C) to visualize details on the anterior surface of two spiders that had been freeze-dried and sputter coated with gold and palladium (80:20).

The image-based measurements allowed us to estimate the volume of each prosoma, chelicera, venom gland and leg. For example, we estimated the volume of the prosoma of a *Schizocosa duplex* (Figs. 1 & 2) as the product of the area of the prosoma's dorsal view ($a_{p,d}$) and the average height of the prosoma, calculated as the area of the prosoma's lateral view ($a_{p,l}$) divided by the length of the prosoma ($l_{p,d}$). Thus the estimated volume of the prosoma (v_p) is

$$v_p = a_{p,d} \cdot (a_{p,l}/l_{p,d}).$$

If the prosoma were rectangular in three planes, this measure of v_p would accurately reflect the structure's true volume. The fact that the prosoma is not rectangular means that v_p overestimates its true volume.

We applied the same method in estimating the volumes of the prosoma and chelicerae of all of the spiders and the venom glands of the spitting spiders (Figs. 1–4). To estimate the volume of the legs of all of the spiders and the venom glands of the wolf spiders, we assumed these structures to be approximately cylindrical. Thus we estimated the volume of a leg (v_l), for example, by taking its area (a_l) divided by its length (l_l) as double its average radius (r_l), and then calculating volume as

$$v_l = l_l \cdot \pi\, r_l^2.$$

One of the wolf spiders in the study was

missing one of its chelicerae and four of the spitting spiders were missing a single leg each. In each of these cases we assumed that the missing structure had the same dimensions as its contralateral mate. Although we measured opisthosomal volumes and masses, we have ignored these measurements in the present study. This is because, as the part of the body that is most extensible (Foelix 1996), it is most subject to the volume and mass fluctuations that accompany changes in feeding history and reproductive state and thus is less likely to provide reliable comparative data.

RESULTS

Morphometry.—The representatives of the two families of spiders were not significantly different in size as measured by the width of the carapace (*Scytodes*: 2.78 ± 0.17 mm, mean ± SE; *Schizocosa*: 2.43 ± 0.057 mm; $t = 2.06$, $P = 0.053$), the mass of the body not including the opisthosoma (*Scytodes*: 17.5 ± 1.93 mg; *Schizocosa*: 19.2 ± 1.26 mg; $t = -0.77$, $P = 0.448$), and the volume of the body not including the opisthosoma (*Scytodes*: 22.26 ± 2.76 mm^3; *Schizocosa*: 21.63 ± 1.02 mm^3; $t = -0.23$, $P = 0.822$). These data confirmed our initial assumption that the two groups of spiders were grossly similar in size.

For some structures (e.g., the legs and the prosoma), we had measures of both mass and volume. Not surprisingly, these measures were closely correlated but not identical, with higher correlations in the spitting spiders than in the wolf spiders (Fig. 5). These highly significant correlations suggest that the use of volume measurements as proxies for mass measurements is justified. As noted above, this substitution is also necessitated by the difficulties encountered in accurately weighing very small structures such as the chelicerae of the spitting spiders and the venom glands of the wolf spiders.

Despite the similarity in the overall sizes of the spitting and wolf spiders, we found striking differences in the sizes of their component parts (Table 1). The average spitting spider had a 36% larger prosoma and had venom glands that were 32 times as voluminous than those of the average wolf spider. The venom glands of *Scytodes* were also, as noted in the literature, conspicuously more complex in shape than those of *Schizocosa* (Fig. 6). At the same time, the legs and chelicerae of *Scytodes* were 42% and 83% smaller, as measured by volume, than those of *Schizocosa*, respectively. The linear dimensions of the legs and chelicerae, of interest in part because they have implications for biomechanical strength, also revealed major differences (Table 1). The legs of the spitting spiders were 42% longer, but 38% less wide in the dorso-ventral direction, than those of the wolf spiders. The chelicerae of *Scytodes* had about the same ratio of length to width (1.84: 1) as the chelicerae of *Schizocosa* (1.79: 1), but were 46% shorter and 41% narrower. Finally, the fangs of the spitting spiders were only 21% as long as the fangs of the wolf spiders (compare Figs. 3 & 8, showing *Schizocosa*, with Figs. 10 & 11, showing *Scytodes*).

Resource allocation.—Several of the conspicuous differences in the allocation of resources by these spiders are readily visible (Figs. 7–11). A wolf spider's chelicerae, for example, are proportionately much more massive relative to the rest of its "face" than are the chelicerae of the spitting spider. In fact, the legs and jaws, together, in the spitting spiders comprise only 22% of the total volume of the measured structures while in the wolf spider they comprise 44% (Fig. 12). In contrast, and as expected from the data in Table 1, the venom glands in *Schizocosa* comprise only 0.3% of the total (0.6% of prosomal volume) while in *Scytodes* they comprise nearly 10% (15% of prosomal volume).

Another component of the resource allocation differences can be seen in a comparison of the anterior four legs to the posterior four legs (Table 1). With respect to leg lengths, the spitting spiders have, on average, 37% longer forelegs than hind legs while the wolf spiders' forelegs are 25% shorter than the hind legs. With respect to leg widths, these relationships are reversed: the spitting spiders' forelegs are 9% narrower than their hind legs while the wolf spiders have forelegs that are, on average, 15% broader (in the dorsal-ventral direction) than the hind legs.

DISCUSSION

When capturing prey, the wolf spider, *Schizocosa*, grabs and bites, often using all eight legs in the grab and enveloping the prey in a leggy basket, or it may hang on to a prey item and hold it at a safe distance using the scopular hairs found on the tarsi and metatarsi,

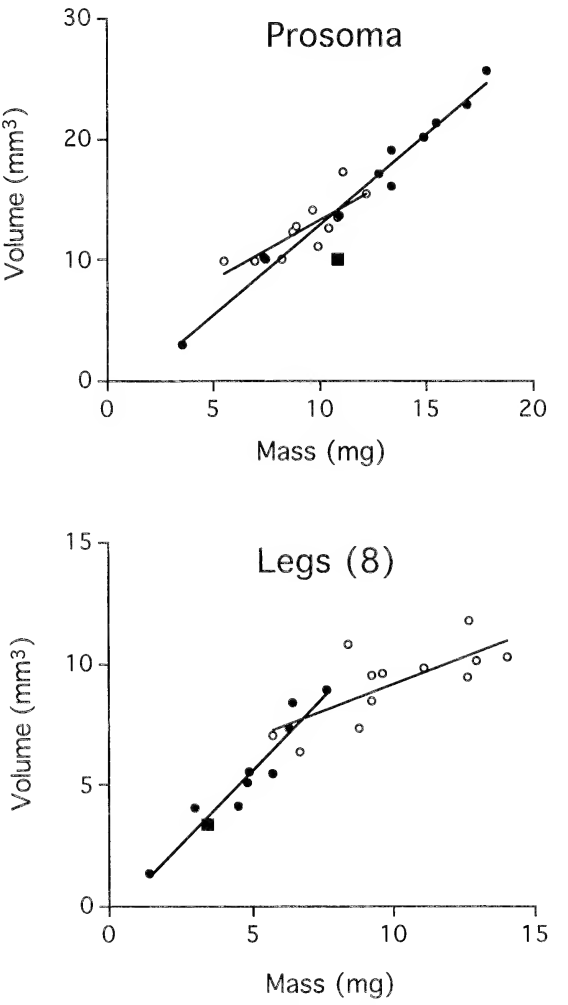


Figure 5.—Relationships between volumes (source: images) and masses (source: balance) for the prosoma and legs of *Scytodes* (filled symbols) and *Schizocosa* (open circles). For the spitting spiders, masses and volumes of both body parts were strongly correlated (prosoma: $r = 0.991$, $P < 0.0001$; legs: $r = 0.960$, $P < 0.0001$). The correlations were also highly significant but less strong for the wolf spiders (prosoma: $r = 0.827$, $P = 0.0009$; legs: $r = 0.730$, $P = 0.007$). Data from the single *Scytodes fusca* specimen (solid square) were included in the two calculations of r for *Scytodes*.

as demonstrated experimentally by Rovner (1978, 1980). The first pair of legs is particularly important for these tasks. The spitting spider, *Scytodes*, enmeshes its prey in a toxic and gummy silk ejected from the spider's fangs, then bites after the prey is immobile. Not surprisingly, these contrasting prey capture techniques are associated with different supporting morphology (Table 1, Figs. 6–11).

Consider the legs. Strength in these appendages is crucial for the wolf spiders whereas sensitivity to position and to the characteristics of what is touched are crucial for the spitting spiders. Strength (resistance to bending) of a tubular structure such as a spider's femur is directly proportional to the fourth power of the radius, inversely proportional to the length and, of course, varies with the properties of the constituent material (Vogel 1988). Thus it is not surprising that *Schizocosa*'s legs are substantially more voluminous than those of *Scytodes*, that their average width (in the direction most crucial for resisting dorso-ventral loading) is 61% greater, and that they are shorter (Table 1). Given that the first pairs of legs are often the ones most used in holding

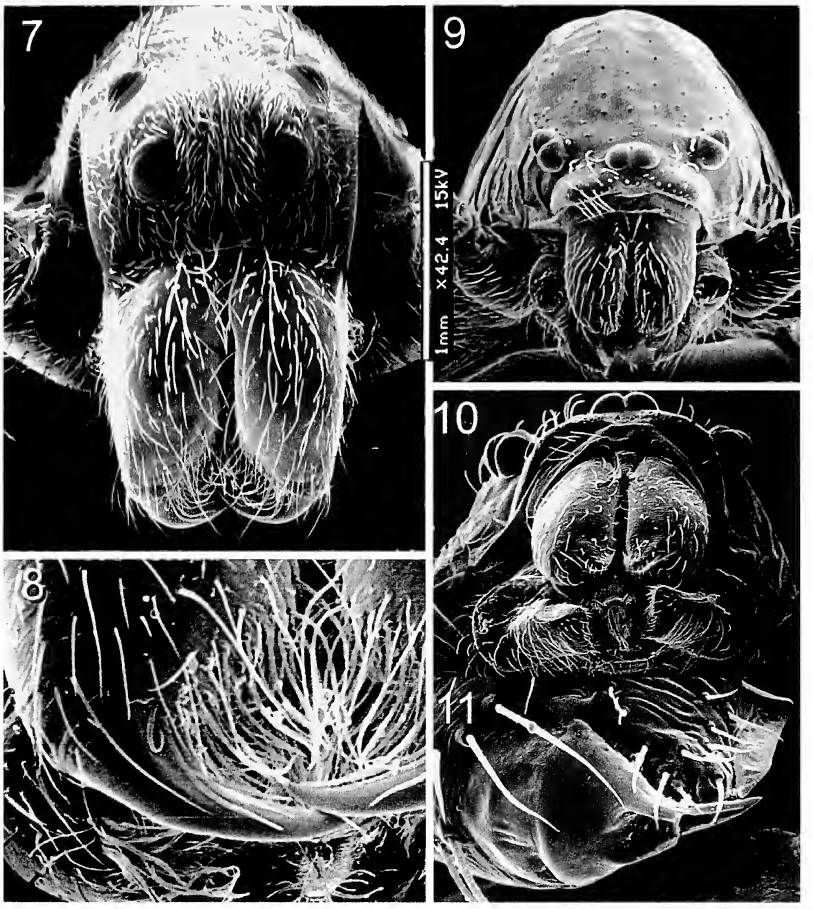
Table 1.—Volumes and linear dimensions of the component parts of the bodies (excluding the opisthosoma) of spitting spiders and wolf spiders. The widths (*) of legs represent mean width, from the dorsal to the ventral surface. The widths (*) of chelicerae represent mean width, from the lateral to the medial surface. We used 2-tailed *t* tests unless we knew from preliminary observation or from the literature to expect a difference in a particular direction.

Component	Measure	*Scytodes* Mean ± S.E.	*Schizocosa* Mean ± S.E.	Comparison		
				t	*P*	Type
Prosoma + legs (8)	volume	22.26 ± 2.76 mm^3	21.63 ± 1.02 mm^3	0.228	0.8218	2-tailed
Prosoma	volume	16.88 ± 2.09 mm^3	12.42 ± 0.68 mm^3	2.186	0.0409	2-tailed
Legs (8)	volume	5.37 ± 0.74 mm^3	9.21 ± 0.46 mm^3	4.544	<0.0001	1-tailed
Chelicerae (2)	volume	0.12 ± 0.01 mm^3	0.69 ± 0.06 mm^3	8.035	<0.0001	2-tailed
Venom glands (2)	volume	2.45 ± 0.35 mm^3	0.08 ± 0.01 mm^3	7.483	<0.0001	1-tailed
Prosoma	width	2.78 ± 0.17 mm	2.43 ± 0.06 mm	2.06	0.0527	2-tailed
Chelicera	length	0.59 ± 0.03 mm	1.09 ± 0.02 mm	14.24	<0.0001	1-tailed
Chelicera	width*	0.32 ± 0.01 mm	0.55 ± 0.02 mm	7.972	<0.0001	2-tailed
Fang	length	0.13 ± 0.01 mm	0.63 ± 0.02 mm	22.392	<0.0001	1-tailed
Legs (mean)	length	19.61 ± 1.77 mm	13.80 ± 0.65 mm	3.306	0.0035	2-tailed
Legs (mean)	width*	0.18 ± 0.01 mm	0.29 ± 0.01 mm	9.332	<0.0001	1-tailed
Leg ratio (fore/hind)	length	1.377 ± 0.24	0.752 ± 0.02	22.385	<0.0001	2-tailed
Leg ratio (fore/hind)	width*	0.912 ± 0.01	1.153 ± 0.02	10.680	<0.0001	2-tailed

prey (Rovner 1980), it is likewise not surprising that in *S. duplex* the first legs are 25% more stout than the hind legs. Chemical and tactile sensitivity, on the other hand, does not depend on structural strength, but length does confer a greater radius of discovery for the sensory organs on the legs. Thus, for the predatory technique used by spitting spiders, long legs that need not be robust are suitable. All of this, even the tendency of *Scytodes* to have longer forelegs than hind legs (but not the converse tendency in *Schizocosa*), supports the assertion that leg properties constitute part of an adaptive suite of morphological characters that enhance the effectiveness of predation for both groups of spiders.

Chelicerae, and the fangs they bear, can be considered in the same way, although here the role of morphological size in the spitting spiders is less clear. Given the predatory technique of the wolf spiders, mechanically strong chelicerae equipped with teeth and bearing long fangs clearly contribute to a wolf spider's ability to restrain prey until venom is delivered via the fangs (Rovner 1980). But why are the chelicerae of *Scytodes* small but not delicate (they have about the same ratio of length to breadth, 1.84:1, as those of Schizocosa,

Figure 6.—A pair each of venom glands from *Scytodes* (left) and *Schizocosa* (right) shown to scale. The spitting spider glands are shown in lateral (top) and dorsal (bottom) views. The venom glands of the wolf spider are nearly cylindrical. The mass of opaque material occupying much of the lateral view of the *Scytodes* gland is the glandular contents (Kovoor & Zylberberg 1972).



Figures 7–11.—SEM images of *Schizocosa* (7, 8) and *Scytodes* (9–11). The chelicerae and fangs are conspicuous components of the frontal view of the wolf spider but are relatively smaller in spitting spider—the fangs of *Scytodes* are nearly invisible when the spider is not about to spit (9) and can only clearly be seen when viewed from below (10, 11). The scale bar applies only to Figs. 7 & 9.

1.98:1), and why are the fangs so disproportionately small (Table 1)? Although further study will be required to answer these questions, we offer two hypotheses. First, the width of the spitting spider's chelicera probably serves to accommodate the larger than normal venom duct that must conduct a viscous mixture of silk, glue, and venom at high velocity. And second, that the diminutive fang facilitates its very rapid oscillation and, in turn, makes possible the characteristic zigzag pattern (Gilbert & Rayor 1985; Foelix 1996) of silk deposition. If this second hypothesis were correct, fang length would then be a good example of evolutionary compromise, in this case between selection for shortness (facilitating oscillation through a reduction in angular momentum) and selection for increased length (facilitating chitin penetration and, ultimately, venom delivery to the interior of prey items). The resolution of the compromise at a fang length too short for effective penetration of thick chitin may have abbreviated the menu of acceptable prey types for spitting spiders (Nentwig 1985).

Resource allocation.—*Scytodes* allocates much less of its total resource pool to overtly predatory structures (chelicerae, venom glands) than does *Schizocosa* (chelicerae, venom glands, and legs) (Fig. 12). When we include the legs of *Scytodes* in this comparison, perhaps legitimate both because they serve a sensory role in predation and because they may be lost relatively frequently during predation (Ades & Ramires 2002), the disparity between the two patterns of allocation de-

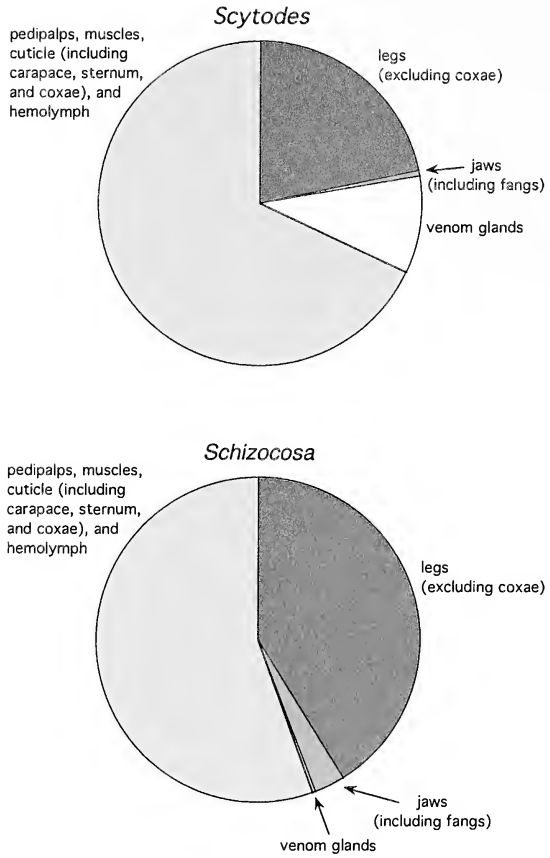


Figure 12.—Mean allocation of resources (as % of non-opisthosoma volume) in spitting spiders (above) and wolf spiders (below). The volume of the grouping of tissues on the left in each chart was estimated by subtraction from the mean volume (excluding the opisthosoma) of the spiders in each species.

creases but remains conspicuous. Moreover, much of the volume of the venom glands of spitting spiders is occupied by secreted products, is not biomass per se, and may be lost to the spider (if recycling does not occur) during predation attempts. Thus spitting spiders employ a predatory technique that appears not to rely on the production and maintenance of large structures.

On the other hand, both spitting and wolf spiders use their legs in locomotion, in mating, and in other activities, so it is not clear that the allocation of resources to legs should be considered as an allocation to predation even when, as in *Schizocosa*, those appendages are entirely necessary for prey capture. If legs are excluded from our consideration, then the fundamental difference between spitting and wolf spiders' allocation patterns is that the former favors the production of venom gland secretions and the latter favors massive chelicerae.

These two views of allocation cannot be reconciled without evaluating them in the context of the phylogeny of the two spider groups, a task that will require further study. For the moment, however, we note the following. First, none of the spider families that are close relatives of the Scytodidae have members that capture prey by spitting, but they do contain members with body plans that resemble those of the spitting spiders (e.g., Pholcidae: Nentwig 1985). And second, many of the spider families that are close relatives of the Lycosidae have members that capture prey by grabbing and biting, and most have body plans that closely resemble that of *Schizocosa*. Further study, then, could reveal that part of the allocation pattern we have described for the spitting spiders is not so much a conse-

quence of their predatory technique as it is a consequence of phylogenetic inertia (Orzack & Sober 2001).

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MATING FREQUENCY IN *SCHIZOCOSA OCREATA* (HENTZ) WOLF SPIDERS: EVIDENCE FOR A MATING SYSTEM WITH FEMALE MONANDRY AND MALE POLYGYNY

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ABSTRACT. Courtship behavior has been studied extensively in the wolf spider *Schizocosa ocreata* (Hentz) (Araneae, Lycosidae). While much research has tested predictions of sexual selection theory regarding male traits and female mate choice, some critical assumptions about female behavior remain untested. To determine if females mate more than once, and to what degree copulation influences subsequent female mating, a multiple mating experiment was conducted. Virgin females were paired randomly with males in laboratory containers. If mating occurred, females were paired with a second male within 24 hr, after 3 days, or after 30 days (enough time for an egg sac to be produced). Of the 101 females tested, 83 (82%) mated with the first male they encountered. The probability of a female mating the first time was not influenced by female size, male size, or male age, but varied significantly with female age post-maturity. Of the 18 males that failed to mate, 3 were cannibalized. Of the 83 males that did mate, 12 were cannibalized after mating. There was no difference between re-mating treatments (1 d, 3 d and 30 d), and analysis of pooled data showed a highly significant difference in the proportion of virgin and mated females accepting males; most females mated only once (93%). In contrast, males appeared to court and attempt mating with every female encountered (virgin and mated), and a majority of males paired with more than one virgin female mated more than once (64.5%). Results suggest that female *S. ocreata* are essentially monandrous, while males are polygynous, and are discussed in the context of potential conflicts-of-interest between the sexes.

Keywords: Lycosidae, *Schizocosa*, mating systems, monandry, polgyny

Female mate choice may be expected to vary depending on the mating system of the species (Arnold 1994; Arnold & Duvall 1994; Lorch 2002). Spider mating systems, like all mating systems, are constrained by several factors: (1) whether males are able to mate multiply; (2) whether females will mate with more than one male; and (3) the nature of sperm storage and fertilization (Austad 1984; Eberhard 1985, 1996; Elgar 1998). Numerous studies suggest that the evolution of male and female mating behavior (male competition, mate guarding, cohabitation, multiple mating) may be influenced by sperm precedence patterns arising from the morphology of the reproductive tract of the female (Austad 1984; Eberhard 1985), although recent studies have revealed exceptions (Eberhard et al. 1993; Watson 1993; Eberhard & Cordero 1995; Elgar 1998; Uhl 1994, 1998; Schaefer & Uhl 2002). Studies of linyphiid spiders, for example, demonstrate that most females mate more than once and multiple paternity broods are common (Martyniuk & Jaenicke 1982; Austad 1982; Watson 1990, 1991a, b). While many studies have shown varying degrees of polygyny and polyandry in spiders (Austad 1984; Eberhard 1985, 1996; Elgar 1998), Singer & Riechert (1995) found a primarily monogamous mating system in a desert agelenid spider, as a consequence of high travel costs to males and a significant decline in female receptivity after the first mating.

The mating strategies and courtship communication of jumping spiders and wolf spiders have been studied extensively (see reviews in Richman 1982; Richman & Jackson 1992; Jackson & Pollard 1997; Hebets & Uetz 1999, 2000; Uetz 2000; Uetz & Roberts 2002). Male salticids and lycosids often perform elaborate visual and/or vibratory courtship displays to elicit female receptivity, and male color patterns, leg decorations and vibration displays often serve as condition-in-

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dicating traits subject to female mate choice (Jackson 1980, 1981, 1986; Clark & Uetz 1992, 1993; Mappes et al. 1996; Parri et al. 1997; Kotiaho et al. 1998; Uetz 2000). The courtship behaviors of wolf spiders in the genus *Schizocosa* have been studied in detail (Mongomery 1903; Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983, 1986; Stratton 1997; Miller et al. 1998; Hebets & Uetz 1999, 2000). Males within this genus display considerable variation in foreleg ornamentation as well as courtship communication, and there is evidence of co-evolution between male signals and female sensory design (Hebets & Uetz 1999, 2000).

Male courtship behavior and female mate choice have been studied extensively in the brush-legged wolf spider *Schizocosa ocreata* (Hentz 1844) (see reviews in Uetz 2000; Uetz & Roberts 2002). Several studies have focused on visual cues provided by the presence of male foreleg tufts in this species, and their role in female mate recognition and preference (Scheffer et al. 1996; Uetz et al. 1996; McClintock & Uetz 1996). The role of tufts in male-male competition is unclear, as studies have produced mixed results. One study has shown that both naturally-occuring and experimental asymmetry in tufts affects the outcome of male-male contests (Uetz et al. 1996), while another study of males competing for females (triad mating experiments) has demonstrated that removal of tufts has no influence on mating success (Scheffer et al. 1996). Other studies suggest that tufts and leg waving displays may exploit a pre-existing sensory bias of female *Schizocosa* (McClintock & Uetz 1996), or serve as amplifiers (Hasson 1989, 1991; Taylor et al. 2000) of condition-indicating male behaviors or traits (Hebets & Uetz 2000). Recent studies have suggested that the relative size of male tufts may serve as a condition-indicating trait (Uetz et al. 2002).

Despite intense interest in sexual selection and especially female mate preference in lycosids, much empirical work has focused on male traits; i.e., differences in expression and the mating advantages of males with increased ornamentation via female mate choice (Hebets & Uetz 2000; Uetz et al. 2002). Perhaps because attention has been focused more on male traits and less on female preference, some critical assumptions regarding reproductive behavior in this lycosid model system remain untested. For example, while often assumed, it is currently unknown whether female *S. ocreata* mate with more than one male. Given high densities and a high rate of male-female encounter in the field (Aspey 1976; Cady 1984) as well as the presence of elaborate male secondary sexual characteristics (and their role in mate choice), theory would predict a promiscuous mating system in this species (i.e., both males and females mate multiply). In this study, we address this gap in our knowledge and test this hypothesis by conducting experiments to investigate whether female *S. ocreata* mate with more than one male and what variables affect female reproductive behavior.

METHODS

Immature *Schizocosa ocreata* were collected from the Cincinnati Nature Center Rowe Woods site (N39°09.904′; W84°15.377′) in Clermont County Ohio, through April and May 2000. Spiders were brought back to the lab and housed individually under identical, controlled conditions (13hrs:11hrs light/dark cycle, temperature 23–25 °C and stable humidity). Spiders were raised to maturity in individual opaque plastic deli dish containers (11.5 cm diameter, 6.2 cm height). Constant moisture was provided via a cotton dental wick inserted through a hole on the bottom of the container and immersed in a dish of water below. Spiders were fed 2–3 subadult crickets (*Acheta domestica* L.) twice a week. Daily checks for molting determined the exact date of maturity, which was recorded for every spider.

To determine if females mate more than once, and to what degree copulation influences subsequent female mating, a multiple mating experiment was conducted. Virgin females (n = 101) were paired randomly with males, and if mating occurred, females were assigned to one of three re-mating treatments: (1) paired within 24 hr; (2) paired after 3 days; (3) paired after approx. 30 days (by which time 50% of females had produced egg sacs). These time intervals were chosen to account for a high rate of male-female encounter in the field (and the possibility of refractory periods in female propensity to re-mate), and/or the possibility that females may re-mate to obtain sperm for a second egg sac. If females

produced egg sacs, these were taken away before any re-mating attempt. Females that did not mate with the first male encountered were paired the next day with a different male. If a female did not mate after three pairings, that female was excluded from the experiment. Females were placed individually in a plastic box with filter paper lining the bottom (12cm x 17cm floor x 5cm walls) for one hour, after which a male was introduced. This allowed the females to acclimate and lay down silk and/or pheromones prior to the introduction of a male. All pairings were videotaped from above. While pairings were random, approximately one-third of males (n = 31) were paired with more than one female to test for multiple mating by males.

Data were analyzed using a contingency test with re-mating treatment (1 d, 3 d and 30 d) as the factor, and mating outcomes (mated once, mated twice) as the response, to determine if mating a second time was dependent on the mating treatment. These data were then analyzed using a McNemar's chi-square test for significance of changes, which is appropriate for paired samples (Zar 1999). Specifically, we tested the null hypothesis that the proportion of females mating with a second male is the same as the proportion of virgin females that mate with the first male they are paired with.

At the end of the experimental studies, spiders were humanely sacrificed using CO_2 anesthesia and preserved in 70% ethanol. After preservation, all individuals were digitally photographed with a Pixera 1.2 mega-pixel digital camera through a Wild M5 microscope. Measurements of individuals were then taken using the UTHSCSA ImageTool program (developed at the University of Texas Health Science Center at San Antonio, Texas and available from http://www.maxrad6.uthscsa.edu). Prosoma width, a widely used measure of body size, was determined for both males and females. Male tuft area and leg length were also measured. All egg sacs produced were preserved in 70% ethanol and dissected open using fine point scissors. All eggs were counted under a dissecting microscope (Wild M5).

The data set consisted of the following individual and pairing variables; age at time of pairings, whether the female ate the first male after mating, size measurements (prosoma width of females and males, male tuft area and leg length), duration of first copulation (if mating occurred), date of egg sac production and number of eggs produced. A preliminary analysis revealed that male prosoma width, tuft size and leg length were highly inter-correlated (Pearson correlations: prosoma width*tuft area, $r = 0.723$, $P < 0.001$; prosoma width*leg length, $r = 0.713$, $P < 0.001$; tuft area*leg length, $r = 0.729$, $P < 0.001$). As intercorrelation of so many independent variables violates a basic assumption of multiple-factor regression models, we chose prosoma width for male size measurement in all subsequent analyses, and scaled male tuft size relative to prosoma width. We used stepwise logistic regression analyses (Hardy & Field 1998) to test the effects of these variables on the: (1) probability of mating with the first male; (2) probability of re-mating; and (3) probability of cannibalism, as in Singer & Riechert (1995). We present the significance level of predictors at the point when they were eliminated from the stepwise regression. Final models only contain significant predictors, thereby providing the most economic combination of initial predictors (Hardy & Field 1998). We also present 'lack of fit' ('LOF') statistics, which test for inappropriate model form. A significant LOF indicates an inappropriate model form. We also used multiple stepwise linear regression analyses to test the effect of the variables on (1) copulation duration; and (2) the number of eggs produced.

RESULTS

Of the 101 females tested, 83 (82%) mated with the first male with which they were paired (Table 1). The probability of a female mating the first time was not significantly influenced by female size, male size, male relative tuft size or male age, but decreased significantly with female age (Table 2). Of the 18 males that failed to mate, three were cannibalized by the female. Of the 83 males that did mate, 12 were cannibalized by the female after mating. Damage to the cannibalized males made accurate measurement impossible and so further analysis of these data was not possible. These rates of cannibalism are similar to results of another study (Persons & Uetz, unpub. data).

Copulations lasted 80–550 minutes (n = 84, median = 155 min) and were not normally distributed (Shapiro-Wilk test, W = 0.813, P

Table 1.—Mating and re-mating frequencies of female and male *S. ocreata*.

	n	Mate (%)	Not
Virgin females:	101	83 (82.18)	18
Previously-mated females:			
1) after 1 day	27	3 (11.11)	24
2) after 3 days	24	2 (8.33)	22
3) after 30 days:			
w/egg sac	16	0 (0.0)	16
no sac	16	0 (0.0)	16
Pooled	83	5 (6.02)	78
Virgin males:	64	49 (76.56)	15
Previously mated males:	31	20 (64.52)	11

Table 2.—Results of stepwise logistic regression elimination analysis of the probability of virgin female *S. ocreata* mating with the first male.

Variables	*df*	χ^2	*P*
Eliminated predictors			
Female size	1	0.095	0.758
Male tuft size	1	0.447	0.506
Male size	1	1.242	0.265
Male age	1	2.440	0.118
Final model			
Female age	1	8.400	0.004
Lack-of-fit	28	31.643	0.326

< 0.001). The duration of copulation (ln transformed) was not significantly influenced by male age ($F < 0.001$, $P = 0.995$), male size ($F = 0.305$, $P = 0.583$), female age ($F = 0.002$, $P = 0.965$), or female size ($F = 1.043$, $P = 0.310$).

Most females mated only once; only a small percentage (7%) of females mated twice (Table 1). The data from the re-mating treatments (1 d, 3 d and 30 d) were analyzed with a contingency test, which revealed no significant difference between mating treatments ($X^2 = 3.89$, $P < 0.284$), and provided justification for pooling the data (Table 1). Results from the McNemar's chi-square test of pooled data showed a highly significant difference in the proportion of virgins and mated females accepting males ($X^2 = 51.429$, $P < 0.001$). In contrast, all males observed ($n = 95$) appeared to court and attempt mating with every female encountered (virgin and mated). Of males paired only once ($n = 64$), a majority (76.56%) successfully mated (Table 1). For those males paired with more than one virgin female ($n = 31$), almost two-thirds (64.5%) mated more than once (Table 1).

The probability of a female re-mating did not vary with treatment, size or relative tuft size of her first mate, her size or age, or second male tuft size, but did increase with the size of the second male (Table 3). Three of the five females that re-mated did not show receptivity displays before being mounted, as is usually the case (Montgomery 1903; Scheffer et al. 1996). All of these re-mated females had shown receptivity displays before accepting their first mate.

Of the five females that re-mated, none cannibalized the male after mating. Of the 78 females that refused to mate a second time, seven (8%) cannibalized the male. The probability that the female cannibalized the male was not influenced by the second male's age, the second male's size, latency between first and second male encounters or female size, but did increase with age of the female at her first mating (Table 4).

Of the 83 females that mated, 50 (60.2%) produced egg sacs, similar to previous observations (Stratton & Uetz 1983; Uetz, unpubl.). Number of eggs produced ranged from zero (no developed eggs) to 82 ($n = 50$, mean = 37.78, SD = 18.59) and was normally distributed (Shapiro-Wilk test, W = 0.978, $P = 0.653$). The number of eggs in the egg sac was not related to female age, male size, whether the female had mated once or twice or age of first mate but approached a significant positive relationship with female size (Table 5).

Table 3.—Results of stepwise logistic regression analysis of the probability of previously-mated female *S. ocreata* mating a second time.

Variables	*df*	χ^2	*P*
Eliminated predictors			
Size of first mate	1	0.088	0.766
Tuft size of first mate	1	0.145	0.703
Male age	1	0.043	0.836
Male tuft size	1	0.088	0.766
Female age	1	0.334	0.563
Female size	1	1.486	0.222
Final model			
Male size	1	5.414	0.027
Lack-of-fit	45	38.498	0.742

Table 4.—Results of stepwise logistic regression analysis of the probability of a previously-mated female *S. ocreata* cannibalizing the second male.

Variables	*df*	χ^2	*P*
Eliminated predictors			
Second male age	1	0.001	0.989
Second male size	1	0.180	0.671
Latency between first and second male encounters	1	0.570	0.450
Female size	1	0.856	0.355
Final model			
Female age at first mating	1	4.620	0.032
Lack-of-fit	21	13.97	0.871

DISCUSSION

While more data are needed on the potential for multiple mating in the field, this laboratory study has demonstrated that female *S. ocreata* appear to be essentially monandrous. Males, on the other hand, are capable of mating multiple times, and are potentially polygynous. Sexual conflict over multiple mating may therefore be inevitable, given differences in the reproductive investment by each of the sexes (Trivers 1972). If a female receives enough sperm from a single copulation to fertilize her eggs, there may be no motivation for a female to mate a second time. Additionally, mating may be a costly activity for females since copulation duration is relatively long, and could lead to loss of foraging opportunities and possibly increased risk of predation and parasite transmission (Scheffer 1992). Females would therefore be expected to exercise a higher degree of mate discrimination than males, and there is some evidence that females of this species exhibit mate choice (McClintock & Uetz 1996; Uetz & Smith 1999; Uetz 2000). However, because males have so much to gain from additional matings, selection would favor mating with highly-resistant previously-mated females, even if it is against the female's interests.

Table 5.—Results of linear regression analysis of the relationship between number of eggs and female and male independent variables.

Variables	*df*	*F*	*P*
Eliminated predictors			
Female age	1	0.032	0.859
Male size	1	0.378	0.543
Female mated more than once	1	0.543	0.466
Female age at first mating	1	1.170	0.287
Final model			
Female size	1	3.630	0.063

There is some evidence in spiders that females may be able to improve the proportion of surviving offspring by choosing a high-quality mate, or by mating with multiple males (Watson 1998). On the other hand, if females are primarily monandrous, males will fertilize most or all of the eggs of each female they copulate with. Female *S. ocreata* most often produce a single egg sac with 30–50 eggs (additional egg sacs are sometimes produced; Uetz persl. obs.), which for the sake of argument might represent an estimate of maximum lifetime reproductive potential. As a consequence, for every female mated, male reproductive potential grows by an amount equivalent to that female's entire reproductive potential, as suggested by Bateman (1948). However, as this species appears to have a 1:1 sex ratio (based on results of lab rearing studies and adult population surveys in the field during the breeding season; Uetz unpubl. data), it then follows that for every male that mates more than once, others will fail to mate at all, or perhaps be cannibalized in the attempt. Variation among females in reproductive success may or may not be smaller than that among males (Bateman 1948; Arnold & Duvall 1994; Lorch 2002); however from a functional perspective this does not make it any less important.

Female monandry would be expected to select for a high degree of choosiness, but in this study 83% of females mated with randomly paired males, and the only significant predictor of mating probability was female

age post-maturity. This result may seem paradoxical, given previous studies of female choice in *S. ocreata* (McClintock & Uetz 1996; Uetz 2000; Uetz & Roberts 2002), but might be explained by several possibilities. This was a "no choice" experiment in laboratory containers where females received both visual and vibratory cues from male courtship. These conditions are unlikely in the field, and females exercising mate choice based on male traits like tuft size or courtship vigor could easily avoid further contact with less favored males. Additionally, as these spiders were collected as sub-adults and maintained under laboratory conditions for several weeks, it is probable that laboratory-housed males were in better condition than their counterparts in the field. Even so, female discrimination based on male characteristics not measured in this study cannot be excluded. In any case, these findings suggest that if the male meets some threshold criterion and a female is physiologically ready, mating will most likely occur.

If mating a second time is not in the best interest of the female, selection would favor resistance and/or avoidance of mating attempts by males, leading to a mating system with female monandry. Water striders provide an example in which sexual selection on mating behavior and morphology is a result of females seeking to avoid matings that may be costly in terms of predation risk or energy expenditure (Rowe et al. 1994; Arnqvist 1997). The importance of coercive matings in a variety of groups, especially arachnids and insects, is becoming increasing clear (Choe & Crespi 1997). While it was not possible to collect accurate data on male copulation attempts for our entire dataset, there is evidence that at least some males may attempt to force reluctant females to copulate. Although our sample size is small, results of the re-mating analysis revealed that second male size was the only significant predictor of mating with a mated female. Of the five previously-mated females that mated a second time, three did not show receptivity displays, and mated only after males "pinned" them down. Male size was a significant predictor in the analysis, suggesting that the largest males may use size to their advantage in mating with resistant females.

It is also possible that reduction in female receptivity after mating is the result of some form of chemically-mediated mechanism on the part of one sex or the other, although this explanation remains highly speculative at this time. There are studies in spiders and other arthropods documenting male manipulation of female reproductive behavior through seminal product transfer during copulation (Riemann et al. 1967; Chapman et al. 1995; Eberhard & Cordero 1995). Males that successfully render a female unreceptive to other males will have fitness benefits through exclusive paternity. This could be considered a form of "post-copulatory mate guarding", and might be mediated by male seminal fluids interacting with the physiology of the female reproductive tract (Eberhard & Cordero 1995). Additionally, since *S. ocreata* are entelegyne spiders, the first male to copulate with a female may be the principal sire of the offspring produced. Testing male preferences between mated and virgin females may give some insight into whether or not males prefer virgin females and/or actively avoid mated females. An alternative might be that mated females produce an 'anti-aphrodisiac', like the compound produced by mated female *Drosophila* to advertise their status and thereby avoid male courtship (Scott & Jackson 1990). Such an adaptation may be advantageous if male courtship decreased the amount of time a female can spend feeding or if male displays attract predators. Since all the males in this study appeared to court, this possibility seems doubtful, but given that males did not have the opportunity to escape, courtship may be a 'last ditch' effort to avoid cannibalism.

In most species, there appears to be some conflict between the sexes over the outcome of mating events (Brown et al. 1997), and results of this study indicate that potential for conflict in *Schizocosa ocreata* wolf spiders as well. While much is yet to be learned about the reproductive biology of *S. ocreata*, results presented here suggest that female monandry and male polygyny, characteristics of only a few spider mating systems studied so far (Eberhard 1985, 1996; Elgar 1998), may apply to this species. These results must be interpreted with caution, however, as they represent outcomes of laboratory studies in simple enclosed containers, and conditions are obviously different in the complex leaf litter environment of the natural habitat. Even so, confirmation of assumed mating systems will

allow more robust predictions in future studies of mate choice.

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DAY VS. NIGHT SAMPLING FOR SPIDERS IN GRAPE VINEYARDS

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ABSTRACT. We compared day sampling (between 0700 and 1100) and night sampling (between 1900 and 2300) of spiders on grapevines in a California vineyard in 1993 and 1994, shaking spiders from the vines onto a drop cloth and vacuuming them up. Pooled density of the seven most abundant spider species did not differ significantly between day and night sampling, nor did density of *Cheiracanthium inclusum* (Miturgidae), *Trachelas pacificus* (Corrinidae), *Oxyopes* spp. (Oxyopidae) or *Neoscona oaxacensis* (Araneidae). Under day sampling *Metaphidippus vitis* (Salticidae) was 60% more abundant and *Hololena nedra* (Agelenidae) more than 2.5 fold more abundant than under night sampling. Daytime sampling generally resulted in a higher percentage of capture for each spider taxa analyzed, but neither of the diversity indices (Shannon-Wiener, Simpson or Bray-Curtis) showed any difference between day and night sampling. Parameters generated by Taylor's power law indicate a uniform distribution for most spider taxa, which was not affected by sampling time with the exception of *H. nedra*. We suggest that at vineyard sites in California with a similar spider community, sampling can be limited to daylight hours if a sampling method is used which is sufficiently vigorous to dislodge spiders from their resting places.

Keywords: Sampling, night, vineyards, grapes

It is well recognized that many spiders exhibit diel activity patterns (Williams 1962), and therefore, the time of day at which sampling for spiders takes place has been considered by many researchers (e.g., Howell & Pienkowski 1971; Le Sar & Unzicker 1978; Nyffeler et al. 1987; Green 1999). Many species of the "wandering spider" families (e.g., Clubionidae, Miturgidae, Corrinidae) are nocturnal or exhibit periods of nocturnal activity (Marc 1990), which is true for many other spider families as well (e.g., most Araneidae and many Lycosidae) (Foelix 1982). Some families, such as the Salticidae, are almost exclusively diurnal. Others are active during the day as well as night (e.g., Oxyopidae).

Should researchers or pest management practitioners sample at night to obtain accurate estimates of spider density or diversity on vegetation in a given ecosystem? In recent studies, sampling time of day made little difference in spider density, but did affect diversity (Coddington et al. 1996; Dobyns 1997; Green 1999; Sorensen et al. 2002). However, sampling method will almost certainly play a role in determining the need to sample at night. For example, visual inspection that is undertaken exclusively in the day will likely miss the nocturnal spiders which rest in cryptic locations, and therefore a host of researchers using this method have included night as well as day sampling (e.g. Nyffeler et al. 1987). Howell & Pienkowski (1971) found that sweep netting, which primarily collects specimens from the distal end of shoots, favored diurnal hunters such as Salticidae and Thomisidae, when used during the day to sample spiders from alfalfa.

If the sampling method is efficient at collecting active spiders as well as extracting spiders from their resting places, then sampling might be done exclusively in the day, as diurnally active spiders will be easily caught and nocturnal spiders will be dislodged from their resting places. Vacuum sampling methods may achieve this, depending on the suction power and whether the spiders rest on relatively exposed locations on the plant. Using a D-vac, Le Sar and Unzicker (1978)

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found significant temporal variation in the vertical distribution of Tetragnathidae, Clubionidae, Thomisidae and Salticidae on soybeans and Green (1999) found that spider diversity in citrus orchards differed significantly when a D-vac sampling took place in the day compared to the night. These findings suggest that some spiders rested off of the vegetation sampled or that the D-vac suction was not sufficient to dislodge resting spiders from their resting places on the plants.

Beat or shake samples are designed to dislodge arthropods from vegetation; therefore, assuming that spiders are resting on the vegetation, all spiders, whether active or resting, should be sampled equally. McCaffrey et al. (1984), using the limb beat method on apples, found no differences in day vs. night sampling for Thomisidae, Dictynidae or Theridiidae and mixed results for Clubionidae and Salticidae. Unfortunately, their data set relied on just two sampling dates. In a southern hardwood forest using a foliage beating method, Coddington et al. (1996) found no difference in spider density between diurnal and nocturnal sampling. At the same study site Dobyns (1997) found no time of day difference using an intensive sampling strategy (a two-hour sampling effort applied three times per 24-hour period), but found slightly more spiders during the day than night using a less intensive strategy (the two-hour sampling just once per 24-hour period).

Another sampling method which might be effectively used to sample diurnal and nocturnal spiders without the need for round the clock sampling is the use of time-sorting pitfall traps (Alderweireldt 1994), but this method has limitations, as pitfall traps are not a very good estimator of density, and would be more useful for ground dwelling rather than arboreal spiders.

Spiders are the dominant predators on cultivated grapes in California's San Joaquin Valley (Costello & Daane 1999). Two studies have been published which compared sampling methods to estimate spider density on the vines (Costello & Daane 1997; Roltsch et al. 1998), but there have been no comparisons made of day sampling vs. night sampling to determine their effects on estimates of density or diversity. The intent of this study was to compare day vs. night sampling using a single sampling method, the drop cloth, to determine if night sampling is important for estimating spider density or diversity in the grape agroecosystem. We focused on seven spider species which dominated our study site. Of these, *Metaphidippus vitis* (Cockerell 1895) (Salticidae) is diurnal; *Trachelas pacificus* (Chamberlin & Ivie 1935) (Corinnidae), *Cheiracanthium inclusum* (Hentz 1847) (Miturgidae) and *Neoscona oaxacensis* (Keyserling 1864) (Araneidae) are considered nocturnal; and *Hololena nedra* Chamberlin & Ivie 1942 (Agelenidae), *Oxyopes scalaris* Hentz 1845 and *Oxyopes salticus* Hentz 1845 (Oxyopidae) are considered active both day and night.

METHODS

Study site and sampling methods.—Day vs. night sampling comparisons were part of a larger study of spider densities on grapevines with and without ground cover (Costello & Daane 1998). The study site was a table grape vineyard (cv. Ruby Seedless) near Reedley, Fresno County, California. The experimental design was a randomized complete block, with two treatments (ground cover present during the grape growing season vs. clean cultivation) and five replicates of each block. Each treatment plot was 1.4 ha (8 rows wide by 80 vines long). Ground cover had no effect on spider density on the vines overall, and little effect on individual spider species density (Costello & Daane 1998). Because there was no ground cover × sampling time interaction ($P > 0.05$), the data were analyzed for sampling time without regard to ground cover treatment. To test the hypothesis that sampling time of day made a significant difference in the estimate of population density, we took two daytime samples (0700–1100 hours) and two nighttime samples (2000–2400 hours) from each plot (i.e., across ground cover treatments) monthly from May–September in 1993 and 1994 (total of 40 samples). We sampled spiders from the vines as a two-person team and used the drop cloth method, which involved laying a 9 x 3 m muslin sheet on the ground underneath the area covered by the trunk, canes, and foliage of two adjacent vines. For ~30 sec. we shook the foliage and beat the vine trunks with mallets to dislodge spiders onto the muslin sheet, and collected the spiders with battery-powered vacuums. To sample at night, we used battery powered headlamps.

In the study vineyard, the vines were trained to a bilateral cordon, and trellised on a 0.9 m crossarm with 2 catch wires. Rows were spaced 3.6 m wide and vines were spaced 2.4 m within the row. Pesticides used during the 2 year period included the fungicides sulfur, copper and myclobutanil for control of grape powdery mildew, *Uncinula necata* Burrill, and the insecticide sodium fluroaluminate for control of lepidopteran pests.

Statistical analysis.—We analyzed the density of the seven most abundant spider species, grouped into six taxa, each of which comprised at least 3% of the total number of spiders collected. These were *T. pacificus*, *C. inclusum*, *M. vitis*, *H. nedra*, *N. oaxacensis*, and *Oxyopes* spp. *Oxyopes scalaris* and *O. salticus* are grouped together as *Oxyopes* spp. for purposes of the analysis because they cannot be easily distinguished as immatures. In addition, we analyzed the pooled abundance of these seven species. We log transformed the data and analyzed them by repeated measures ANOVA (SAS Institute 2000), using date as the repeated measures variable. Because there was no interaction between sampling time and year for spider density nor diversity ($P > 0.05$), the two year period was analyzed as a complete data set, and sampling dates are presented as the mean julian date of the two sampling years.

Spider species diversity in day vs. night sampling was estimated in several ways. A similarity index was created using the Bray-Curtis measure (Bray & Curtis 1957; Krebs 1989):

$$B = \frac{\sum |X_{ij} - X_{ik}|}{\sum (X_{ij} + X_{ik})}$$

where B = the Bray-Curtis measure of dissimilarity and X_{ij}, X_{ik} = percentage of species i in each sample j (day sample) or sample k (night sample). We have chosen to use this index as a measure of similarity by using the complement of B (i.e., 1—B), as suggested by Wolda (1981). Values of the index range from 0 (completely dissimilar) to 1.0 (completely similar). The Shannon-Wiener index (Southwood 1978), which is sensitive to rare species, was calculated as:

$$H = -\sum p_i \log p_i$$

where p_i is the proportion of the total number of species or genera identified. The Simpson index (Southwood 1978), which is more sensitive to common species, was calculated as:

$$D = 1/\sum p_i^2$$

where p_i, again, is the proportion of the total number of species or genera identified.

To determine the effect of sampling time on spider dispersion, the mean and variance of spider abundance for each sample date (natural log) were used to generate dispersion parameters using Taylor's power law (Taylor 1961):

$$s^2 = a\mu^b$$

where s^2 is the variance, a is a sampling parameter, μ is the mean, and b is an aggregation parameter. The aggregation parameter (b) describes species dispersion: Values of $b > 1$ indicate a clumped distribution, of $b = 1$ a random distribution, and of $b < 1$ a uniform distribution (Taylor 1961).

RESULTS

The spider community on grapes in this vineyard consisted of at least 15 families, comprising 22 identified species, with seven species making up 95% of the community. Over the two year period, a total of 6,410 spiders was collected: 3668 during the day, and 2742 during the night (Table 1). Spider density per vine (the seven most abundant species pooled) did not differ significantly between day and night (Table 2). In addition to the overall counts, the absolute number of spiders collected was higher for every spider taxon during the day (Table 1), but there was no significant difference in spider density with day vs. night sampling of the spiders *C. inclusum*, *T. pacificus*, *Oxyopes* spp. or *N. oaxacensis* (Fig. 1, Table 2). However, for two species there were significant differences ($P < 0.01$) between treatments: *M. vitis* was 60% more abundant under day sampling, and *H. nedra* was more abundant under day sampling by more than 2.5 fold (Fig. 1, Table 2).

For each spider taxon a higher percentage overall was collected in the day than during the night (Table 1). However, this did not have a significant impact on the diversity indices. There was a trend toward higher overall spider diversity early in the season, but there were no significant differences in diversity for ei-

Table 1.—Total number of spiders collected and percentage of spiders collected by sampling time and spider taxon, 1993 and 1994 seasons combined.

Spider taxon	Total number of spiders collected		Percentage of all spiders collected	
	Day	Night	Day	Night
Trachelas pacificus	1424	1214	22.2	18.9
Cheiracanthium inclusum	690	576	10.8	9.0
Oxyopes spp.	630	373	9.8	5.8
Metaphidippus vitis	402	244	6.3	3.8
Neoscona oaxacensis	165	123	2.6	1.9
Hololena nedra	174	63	2.7	1.0
Theridion spp.	63	41	1.0	0.6
Linyphiidae	49	38	0.8	0.6
Salticidae	27	13	0.4	0.2
Thomisidae	19	10	0.3	0.2
Lycosidae	8	19	0.1	0.3
Gnaphosidae	9	16	0.1	0.2
Anyphaenidae	6	9	0.1	0.1
Total spiders	3668	2742	57.22	42.77

ther the Shannon-Wiener index ($P = 0.98$) or the Simpson index ($P = 0.73$) between day and night sampling (Table 3). In addition, the Bray-Curtis similarity index was 0.89, which is considered quite high. No spider taxon was found exclusively during either sampling period.

The spider seasonal abundance pattern (i.e., spider density over time) was not significantly altered by time of day sampling for any spider species except *T. pacificus* (sampling by date interaction: $F = 9.56$, $df = 4, 124$, $P < 0.001$). For this spider, night sampling showed a small early season peak and larger late season peak in density, but only one late season peak for day sampling (Fig. 1). Day and night sampling densities peaked earliest for *N. oaxacensis* and peaked on the last sampling date for *C. inclusum*, *H. nedra* and *Oxyopes spp*. Peak density for *M. vitis* was mid to late season for both day and night sampling (Fig. 1).

Regressions of s^2 against μ were significantly different from zero for every spider taxon and sampling time ($P < 0.002$, Table 4). With one exception, values of b were <1, indicating a uniform distribution for all spiders, which was not changed by sampling time. The one exception was night sampling of *H. nedra*, which produced a value of 1.17 for b, indicating a random distribution.

DISCUSSION

Although the sum total of spiders (all spider taxa combined) was higher under day sampling, we found no overall statistically significant difference in spider density nor diversity

Table 2.—Mean spiders per vine and summary statistics from the analysis of variance, 1993 and 1994 seasons combined.

	Mean spiders per vine		ANOVA		
	Day	Night	*F*	*df*	*P*
T. pacificus	6.47 ± 0.77	5.67 ± 0.44	0.40	1, 31	0.533
C. inclusum	3.13 ± 0.54	2.69 ± 0.44	0.07	1, 31	0.794
Oxyopes spp.	2.86 ± 0.65	1.74 ± 0.34	0.92	1, 31	0.344
M. vitis	1.82 ± 0.18	1.14 ± 0.11	9.36	1, 31	0.004
N. oaxacensis	0.75 ± 0.11	0.54 ± 0.06	2.03	1, 33	0.163
H. nedra	0.79 ± 0.10	0.29 ± 0.04	8.97	1, 31	0.005
Total spiders	15.84 ± 1.86	12.09 ± 1.01	0.67	1, 34	0.420

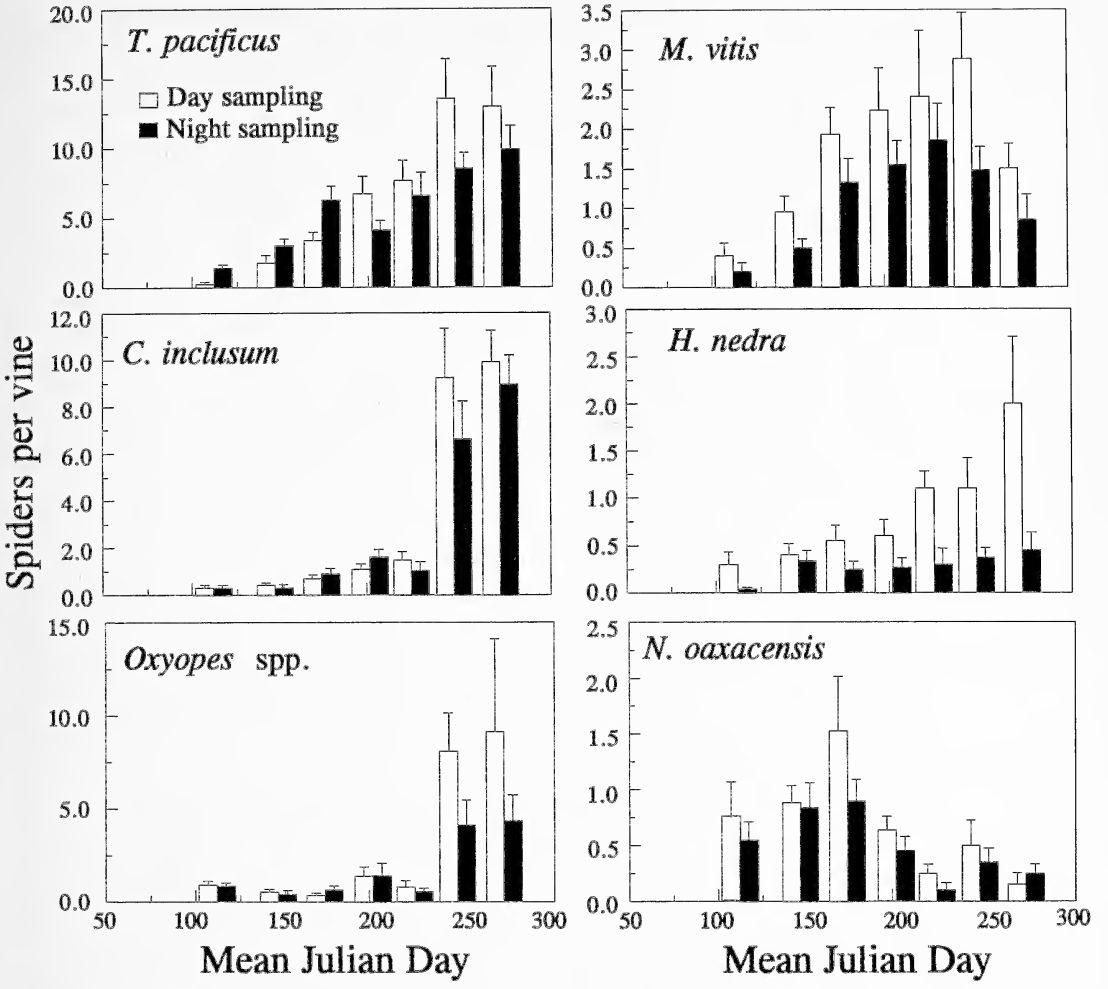

Figure 1.—Spider density per vine of the six most common taxa, 1993 and 1994 data combined, with the julian dates of the two study years averaged. Open bars represent day sampling, and closed bars night sampling. *Metaphidippus vitis* and *H. nedra* showed significantly higher density with day sampling ($P < 0.01$). No significant differences were found in spider density for any of the other taxa.

Table 3.—Shannon-Wiener (H) and Simpson (D) diversity indices, 1993 and 1994 data combined, with corresponding *P*-values.

Mean Julian Day	H		D	
	Day	Night	Day	Night
112	0.83	0.76	5.88	4.52
147	0.93	0.75	6.94	3.89
173	0.79	0.67	4.61	2.94
202	0.71	0.74	3.22	4.09
222	0.61	0.64	2.82	2.94
247	0.68	0.67	3.80	3.46
272	0.65	0.63	3.69	3.28
	$P = 0.98$		$P = 0.73$	

between diurnal and nocturnal sampling. Our findings are similar to other studies which used beating or shaking of vegetation as a sampling method (McCaffrey et al. 1984; Coddington et al. 1996; Dobyns 1997), in that few differences in overall spider density were found with day vs. night sampling. Dobyns (1997) found that spider density was significantly different (more spiders were found during the day) but only for a low intensity sampling method, and concluded that sampling method was more important than sampling time of day. Sorensen (2002) found an interaction between sampling time of day and sampling method, with some methods producing

Table 4.—Regression statistics of ln s^2 against ln μ for generation of Taylor's power law parameters.

Spider	Sampling time	a	b	R^2	P
T. pacificus	Day	0.472	0.502	0.834	0.0001
	Night	0.729	0.447	0.831	0.0001
C. inclusum	Day	0.256	0.720	0.987	0.0001
	Night	0.325	0.599	0.908	0.0001
Oxyopes spp.	Day	0.296	0.434	0.917	0.0001
	Night	0.359	0.399	0.923	0.0001
M. vitis	Day	0.481	0.440	0.666	0.0013
	Night	0.278	0.599	0.795	0.0001
H. nedra	Day	0.285	0.458	0.778	0.0002
	Night	0.056	1.165	0.743	0.0004
N. oaxacensis	Day	0.300	0.393	0.705	0.0007
	Night	0.160	0.743	0.866	0.0001
All spiders	Day	0.902	0.451	0.821	0.0001
	Night	1.131	0.427	0.825	0.001

higher abundance of spiders at night. Other studies have concluded that sampling method can lead to very different estimates of spider density and diversity (Costello & Daane 1997; Roltsch et al. 1998).

When analyzed by taxon, we found two species, *M. vitis* and *H. nedra*, significantly different in density with respect to time of day sampling, and both of these were more abundant with day sampling. *Metaphidippus vitis*, like most other salticids, is an active diurnal hunter that searches for prey out on the leaves and shoots and can quite easily be shaken off during the day. Could it be that *M. vitis*, and perhaps other salticids, rest during the night in relatively deep crevices, and are therefore more difficult to shake out? For *H. nedra*, finding a logical explanation is more difficult. This agelenid sits and waits for prey to land on the flat, sheet like portion of its funnel shaped web, and presumably, will respond to prey during the day or night. Because *H. nedra* does not leave its web to rest, the explanation for this difference cannot be that it is not as accessible during the night. However, it is possible that behaviorally, its response to disturbance at night is to retreat rather than to flee. We wonder if this might not be related to lower temperatures at night: *H. nedra* is a very quick and agile spider, and perhaps because lower temperatures do not allow it to flee as fast at night, it switches to a retreat response.

Given that the diurnally active hunting spider *M. vitis* was sampled at a higher density during the day, why did we not find parallel results with the nocturnal spiders *T. pacificus*, *C. inclusum* and *N. oaxacensis*? There are two possibilities, the first being that their resting places are on the foliage, rather than in recesses or crevices on the bark of the trunk, or in the leaf litter or soil underneath the vine. This possibility is most plausible for *C. inclusum* and *N. oaxacensis* than for *T. pacificus*. The silken bivouacs of *C. inclusum* are commonly encountered on the foliage of grapevines, and *N. oaxacensis* is well known for stringing its orb web between the rows of grapevines and resting on the foliage during the day. However, this explanation does not fit well with *T. pacificus*. Few bivouacs of this species have been observed on grape foliage, as this spider has a penchant for hiding under the bark of the trunk. This brings us to the second possibility, that *T. pacificus* is not as nocturnal as we thought, and may be just as active during the day as during the night.

Our results do not indicate that estimates of spider diversity are affected by time of day of sampling, in contrast to findings of other researchers. Green (1999) found that generic richness differed significantly with sampling time in over 40% of samples. Coddington et al. (1996) and Dobyns (1997) found some spider species and even entire families only at night, and Sorensen et al. (2002) found species unique to both day and night. The implication is that night sampling was necessary to achieve a more accurate estimate of species richness and a more complete picture of the

spider fauna. The reasons our results differed may have to do with the ecosystem studied: our grape agroecosystem was much lower in species richness than the southern hardwood forest (Coddington et al. 1996), subtropical citrus orchard (Green 1999) or afromontane (Sorensen et al. 2002) ecosystems.

We suggest that in California vineyards with similar spider communities, if a method is used which is sufficiently vigorous to dislodge spiders from their resting places, sampling can be limited to daylight hours. Although we found no difference in spider species diversity between day and night sampling, it is possible that at sites with higher species richness than ours, sampling time of day could influence estimates of diversity. As for species density, there was no under representation of nocturnal spiders, which is the main concern when limiting sampling to daylight hours; each of the two spider species (*M. vitis* and *H. nedra*) which differed between day and night sampling was more abundant with day sampling.

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DETERMINING A COMBINED SAMPLING PROCEDURE FOR A RELIABLE ESTIMATION OF ARANEIDAE AND THOMISIDAE ASSEMBLAGES (ARACHNIDA, ARANEAE)

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ABSTRACT. As the disappearance of species accelerates, it becomes extremely urgent to develop sampling protocols based on efficient sampling methods. As knowledge of the Iberian spider fauna is extremely incomplete, it is becoming necessary to facilitate reliable and complete species richness inventory collection. In this work the results from six sampling methods (sweeping, beating, pitfall traps, hand collecting at two different heights and leaf litter analysis) in three habitats with different vegetation structure are compared for the inventory of Araneidae and Thomisidae in 1 km^2 sampling plots. A combination of sweeping, beating and pitfall trapping prove to be necessary to achieve a reliable inventory of these two spider families. Hand collecting above knee level contributes to the improvement of the protocol in certain habitats where araneids, concentrated in patches of suitable vegetation, are easy to find.

RESUMEN. A medida que se acelera la desaparición de las especies se hace más urgente el desarrollo de protocolos de muestreo basados en métodos eficientes. El conocimiento de la aracnofauna ibérica es bastante escaso, por lo que es necesario desarrollar inventarios fiables y tan completos como sea posible, de una manera rápida y sencilla. En el presente trabajo se comparan seis métodos diferentes de muestreo (mangueo, batido, trampas de interceptación, captura directa a dos alturas distintas y análisis de hojarasca) para el inventariado de las familias Araneidae y Thomisidae en parcelas de 1 km^2, estudiando su comportamiento en tres hábitats con diferente complejidad estructural de la vegetación. Los resultados muestran que para conseguir inventarios fiables de estas dos familias es necesaria la combinación del mangueo, batido y de las trampas de caída. En los habitats en los que la localización de los araneidos es sencilla debido a que se concentran en parches de vegetación concretos, la captura directa a una altura por encima de las rodillas contribuye a mejorar el protocolo.

Keywords: Species richness inventory, sampling methods, efficiency, complementarity

Loss of biodiversity, one of the greatest environmental problems (Wilson 1988; May et al. 1995), the outcome of the accelerating destruction of ecosystems, means that many species will be eradicated while still undiscovered or unstudied. Protecting biodiversity implies protecting terrestrial arthropods, a group poorly known but comprising around 80% of the Earth's species and including those denominated as hyperdiverse (Hammond 1992). These groups are the least understood, yet contribute most to the planet's biotic diversity. Conservation of biological diversity requires detailed information on the geographic distribution of organisms. In the case of arthropods, as this information is almost impossible to acquire in the medium-term by means of field sampling (Ehrlich & Wilson 1991; Williams & Gaston 1994), the utilization of predictive model techniques may be the only possible way to estimate the distribution of biodiversity attributes (Margules et al. 1987; Iverson & Prasad 1998; Guisan & Zimmermann 2000; Lobo & Martín-Piera 2002; etc). However, application of these predictive methods requires reliable biological information; when this is lacking, the design of specific sampling protocols for each taxonomic group that gather the maximum information, most cost-effectively, becomes essential.

About 36,000 species of the order Araneae have been described, while the total number is estimated at between 60,000 and 170,000 (Coddington & Levi 1991; Platnick 1999). This is one of the most diversified orders (Coddington & Levi 1991) and offers the greatest potential to help regulate terrestrial arthropod populations (Marc et al. 1999). Ara-

neids, one of the most successful spider families (approximately 2,600 species; Foelix 1996), are relatively easy to detect due to their size, coloration and their orb webs. Vegetation structure seems to be the most important parameter in determining their presence (Wise 1993). Unlike the araneids, thomisids (crab spiders) do not use webs to capture prey; instead they ambush prey from flowers or leaves (Wise 1993), where their cryptic coloration allows them to go unnoticed. Some genera, like *Xysticus* and *Ozyptila*, are eminently edaphic, capturing prey among leaf litter and herbaceous vegetation.

Arachnological tradition is sorely lacking in the Iberian Peninsula, and spider distribution is extremely poorly understood (1,180 recorded species; Morano 2002). Only in the province of Aragón is there a recent catalogue of arachnological fauna (Melic 2000); the rest of the Iberian catalogues include out-dated records, most of doubtful quality and with erroneous data (Melic 2001). So, it is necessary to augment taxonomic and distributional data on Iberian spiders by using effective and standardized sampling protocols, the design of which involves overcoming some difficulties. As spiders' life history, behavior and morphologic, physiological and ecological adaptation vary widely (Turnbull 1973), sampling method effectiveness depends on the nature of the taxonomic group (Canard 1981; Churchill 1993; Coddington et al. 1996; Costello & Daane 1997; Churchill & Arthur 1999). Furthermore, it must be kept in mind that the effectiveness of the method also depends on the environment (Canard 1981). Thus, in order to inventory reliably and completely, the design of the sampling protocol should combine various sampling methods, selecting the methods promising maximum information and complementarity for each environment and taxonomic group (Coddington et al. 1996; Green 1999; Sørensen et al. 2002). In this work, several sampling methods for Araneidae and Thomisidae species are compared, in habitats with distinct vegetation complexity, in order to determine which combination captures the maximum number of species with the minimum number of sampling techniques.

METHODS

Study site.—The study was carried out from 2 May–14 June 2002 in three localities in the Comunidad de Madrid (central Spain), with vegetation differing in structural complexity as follows: 1) A grassland zone subjected to intense pasturing pressure, with small shrub patches, at 980 m elevation in the municipality of Colmenar Viejo (latitude 40.69, longitude −3.77). Its potential vegetation is the holm-oak forest (supra-mesomediterranean-siliceous series of *Quercus ilex rotundifolia*; Rivas-Martinez, 1987). 2) An extensive and dense zone of shrub located in El Berrueco (latitude 39.97, longitude −3.53), at 940 m elevation. The area belongs to the same vegetation series as the former (Rivas-Martinez, 1987); nevertheless, human activity has caused the original vegetation to be replaced by the *Cistus ladanifer* series, with patches of *Lavandula pedunculata* and *Thymus* spp. 3) A Holm-oak forest zone in Cantoblanco (latitude 40.51, longitude −3.65) at an elevation of 700 m, composed of some tall (6–8 m) specimens of *Quercus ballota*, though the majority of the trees are between 3–4 m tall. An old plantation of *Pinus pinea*, which dates from the 1930s, occupies one part of the forest.

Sampling methods.—In each habitat a 1 km^2 sampling plot divided into 2,500 subplots of 400 m^2 was established; 20 of these subplots were chosen at random, and a sampling effort unit carried out in each. For the capture of species in these two families, six cheap, easy and widely used sampling methods were employed: sweeping, beating, pitfall traps, above-knee-level visual search, below-knee-level visual search, and leaf litter analysis. A sampling effort unit was defined as one of the following: 1) A one-person sweep of the herbaceous vegetation and shrub during 15 minutes. The opening of the sweep net was 37 cm in diameter, and it was emptied at regular intervals to avoid loss and destruction of the specimens. 2) A one-person beating of bushes and small trees and branches during 15 minutes with a heavy stick; the specimens fell on a 1.25 × 1.25 m white sheet. In cases where the structure of the vegetation made the use of the sheet difficult a 41 × 29 cm plastic pail was employed. 3) A one-person visual search from knee level to as high as one can reach (above visual search, AVS) during 15 minutes. 4) A one-person visual search from ground to knee level (below visual search, BVS) during 15 min. Stones were lifted up because tho-

misids, especially females after laying eggs (Levy 1975; Hidalgo 1986), from the genera *Xysticus* and *Ozyptila* usually dwell under them. 5) Analysis during 15 min. of leaf litter poured in a white pail, justifiable because this is the habitat of the genus *Ozyptila* (Thomisidae) (Urones 1998). 6) The running of 4 open pitfall traps during 48 hours. These traps were 11.5 cm wide and 1 liter in volume, each 10 m apart from the others in order to avoid interference effects and to maximize the efficacy of each trap (Samu & Lövei 1995). Traps were filled with water, and a few drops of detergent added to break the surface tension so as to prevent the spiders from escaping.

Spiders were sucked up with an aspirator to reduce damage and were transferred to 70% alcohol. Sampling was always done by the same person in order to avoid possible differences due to the effect of the collector (Norris 1999); rainy and windy days were avoided in order to prevent a reduction in the efficiency of the sampling methods (see Gyenge et al. 1997; Churchill & Arthur 1999). All specimens are deposited in the Museo Nacional de Ciencias Naturales collection (Madrid, Spain). All together, sampling involved running 240 pitfall traps (3 sampling plots × 20 subplots × 4 pitfall traps) and one-person fieldwork during 75 hours (0.25 hours × 5 methods × 3 sampling plots × 20 subplots).

Data analysis.—The cumulative number of species found by different sampling efforts (species accumulation curves) was studied to evaluate the accuracy of the species inventories obtained in each of the three sampling plots (see Gotelli & Colwell 2001). The number of sampling effort units (i.e. the number of subplots) was used as the measure of sampling effort, and the order in which sampling unit inventories were added was randomized 500 times to build smoothed curves using the EstimateS 5.0.1 software (Colwell 1997). The asymptotic value of the accumulation curves obtained was estimated using the Clench equation (Soberon & Llorente 1993; Colwell & Coddington 1994). This score, together with the species richness estimations produced by three nonparametric methods, was used to test if the total number of species caught in each sampling plot underestimated the true species richness. The nonparametric species richness estimators used are the first-order jackknife, the abundance-based coverage (ACE), and the incidence-based coverage estimator (ICE). Detailed descriptions of the estimators can be found in Colwell (1997) and Colwell & Coddington (1994).

In order to study the effects of sampling method and the interaction of method and habitat on the number of species and individuals collected per sampling effort unit, a factorial ANOVA was performed. As data were not normally distributed, they were transformed by log(n+1), and a Tukey test (HDS) was used to determine pairwise significant differences ($P < 0.05$). STATISTICA package (1999) was used for all statistical computations.

Other methodological considerations.—As Norris (1999) pointed out, the inclusion of immature specimens is the factor which has the most significant effect on community trends. It cannot be assumed that the abundance distribution of juveniles is the same as that for adults, and the relative abundance of species in a community can be highly altered if juveniles are considered. However, since our objective was to find all the species inhabiting the sampling plots, juveniles that could be identified to the species level were included in the analysis. Sometimes genera represented only by immature states did appear, in which case, they were also included. Rejecting juveniles would have involved rejecting valuable information, and as they increased sample sizes significantly, their inclusion allowed statistical analysis. In araneids and thomisids, unlike in most other spider families, color and morphology facilitate the identification of some juveniles. All together, 942 individuals were captured, 56% of them juveniles; almost half (247 individuals) have been used in the analysis.

RESULTS

In 80 sampling effort units, a total of 661 individuals were captured, representing 26 species, 11 araneids and 15 thomisids.

Completeness of the inventories.—The Clench model function fits the accumulation curves well in each of the three sampling plots, with percentages of explained variation higher than 99% (Table 1 & Fig. 1). The predicted asymptote score does not differ too much from the observed species richness, the percentages of collected species oscillating around 80%. The nonparametric estimators

Table 1.—Observed species richness (S_{obs}) and results of four species richness estimators for each habitat. The relationship between the number of sampling effort units and the number of species was fitted to the asymptotic Clench equation (Colwell & Coddington 1994) where a/b is the asymptote and R^2 the percentage of explained variance. Jackknife 1 (first-order jackknife), ACE (abundance base coverage) and ICE (incidence-based coverage) are nonparametric estimators of species richness (Colwell 1997).

	Forest	Shrub	Grassland
S_{obs}	17	20	15
Clench	a/b = 21.6; R^2 = 99.9	a/b = 25.0; R^2 = 99.4	a/b = 18.8; R^2 = 99.9
Jackknife 1	19.85	26.65	17.85
ICE	18.49	27.18	16.73
ACE	17.85	25.07	17.26

used indicate that the collected species richness varies from 86%–95% for the forest plot, 74%–80% for the shrub plot, and 84%–90% for the grassland plot. These results suggest that the exhaustiveness of the sampling in each of the three habitats is similar, so sampling plot composition and richness figures are comparable. However, still more intensive sampling should be necessary to obtain an accurate inventory in each habitat.

Sampling method performance.—From the three sampling plots, only one individual of *Mangora acalypha* (Walckenaer 1802) was captured by leaf litter analysis method (in the shrub plot). As this species was collected plentifully with the other sampling methods,

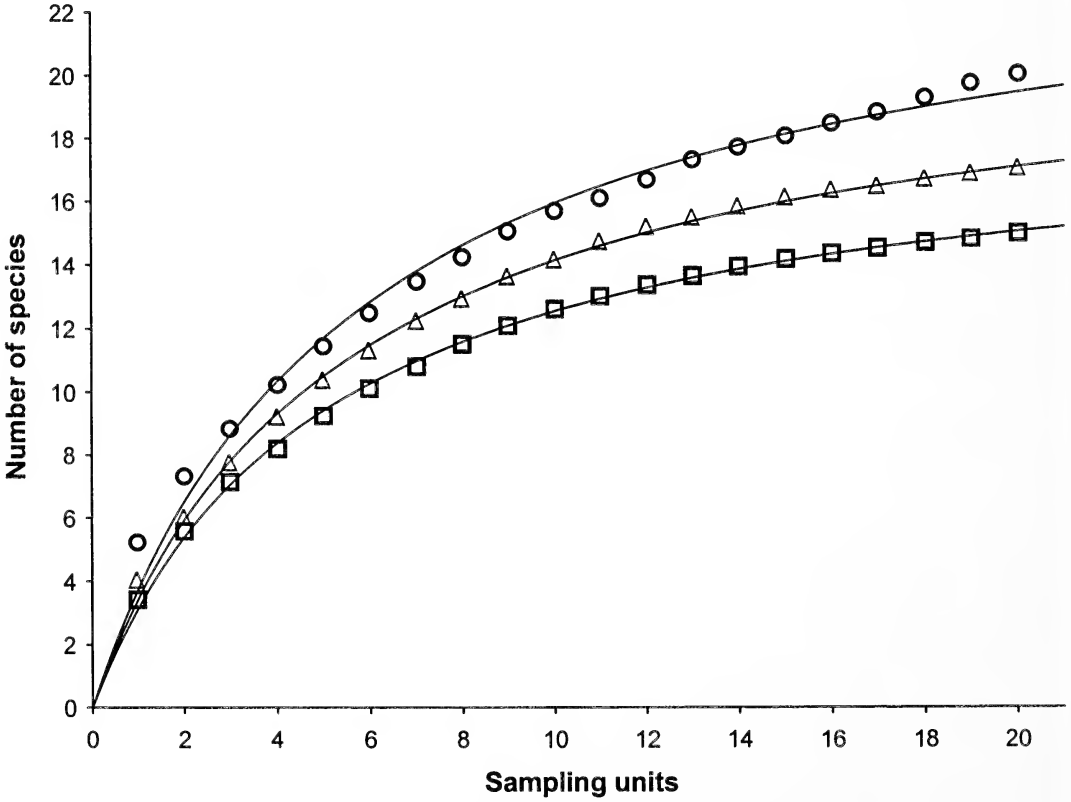

Figure 1.—Species accumulation curves for the three sampling plots with Clench function fitted: □ grassland; ○ shrub; △ forest. The cumulative number of species found at different numbers of sampling effort units was randomized 500 times using the EstimateS 5.0.1 software (Colwell 1997):

Table 2.—Total number of individuals (n), mean number of individuals (± SE) per sampling unit (N_{MEAN}), total number of species (S), mean number of species (± SE) per sampling unit (S_{MEAN}), and number of unique species (S_{UNI}) for each sampling plot and each sampling method.

	Sampling Plot		
	Forest	Shrub	Grassland
n	205	348	108
N_{MEAN}	2.07 ± 0.36	3.48 ± 0.56	1.57 ± 0.5
S	17	20	15
S_{MEAN}	0.92 ± 0.14	1.5 ± 0.17	0.72 ± 0.1

	Sampling Method				
	Pitfall	Sweeping	Beating	BVS	AVS
n	25	442	90	13	91
N_{MEAN}	0.41 ± 0.14	8.08 ± 1.06	1.6 ± 0.23	0.22 ± 0.09	1.55 ± 0.28
S	5	17	15	7	9
S_{MEAN}	0.3 ± 0.08	2.7 ± 0.24	1.08 ± 0.14	0.18 ± 0.07	0.98 ± 0.14
S_{UNI}	2	5	3	0	0

the results of this technique are not considered. Both the mean number of collected species ($F_{(4,285)} = 58.5$; $P < 0.0001$) and the mean number of individuals ($F_{(4,285)} = 79.9$; $P < 0.0001$) differ statistically from one sampling method to another. Both in the case of species richness and for the number of individuals, all pairwise comparisons between sampling methods are significant by a posteriori Tukey HSD test, except in the case of pitfall traps and BVS, and beating and AVS (see Table 2). Sweeping, the technique which captured the greatest number of species and individuals, with araneids making up 47% of the species and 68% of the individuals collected, is also the method that captured more species not captured by any other sampling method (unique species, two araneids and three thomisids). Pitfall traps and BVS are the methods that captured the smallest number of species and individuals, but while BVS did not yield unique species, pitfall traps did capture two unique species. With pitfall traps, only thomisids of the genera *Xysticus* and *Ozyptila* were captured. In the case of the BVS, araneids make up 57% of the species and 62% of the individuals. With regard to the other sampling methods, beating and AVS yield the same number of individuals, though the total number of species is larger for the former. In beating, araneids make up 47% of the species and 43% of the individuals; using AVS araneid, captures were more frequent, accounting for 78% of species and 89% of individuals. AVS did not yield any unique species, while beating produced three unique thomisids.

By an iterative procedure the sampling methods were ranked sequentially, for each habitat, according to contribution to total species richness in this habitat. Both in the forest and shrub, sweeping is the method that yielded more species, followed by beating and pitfall traps. Together, these three methods captured all the observed species in these habitats. In grassland, where a broader combination of methods is necessary to obtain a reliable inventory (Table 3), beating captured more species, while sweeping, AVS and pitfall traps or BVS seem to be indispensable.

Sampling method-habitat interaction.—The mean number of species per sampling unit ($F_{(2,285)} = 15.14$; $P < 0.001$), as well as the mean number of individuals ($F_{(2,285)} = 15.73$; $P < 0.001$), differs significantly between sampling plots. According to a posteriori Tukey HDS test, only in the shrub sampling plot is the species richness and number of individuals significantly greater than in the other two sampling plots (Table 2). However, sampling method and habitat interaction significantly affect both the mean number of species ($F_{(8,285)} = 6.6$; $P < 0.0001$) and the mean number of individuals per sampling unit ($F_{(8,285)} = 9.6$; $P < 0.0001$), indicating that the performance of the various sampling methods depends on the habitat.

The results of a posteriori Tukey HSD test highlight the significantly different interaction

Table 3.—Results of a complementarity procedure in which the inventories of each sampling method were sequentially selected for each habitat according to its contribution to the species richness.

Habitat	Iteration	Sampling method	Number of species	Accumulated species
Forest	1	Sweeping	12	12
	2	Beating	4	16
	3	Pitfall	1	17
Shrub	1	Sweeping	13	13
	2	Beating	4	17
	3	Pitfall	3	20
Grassland	1	Beating	8	8
	2	Sweeping	4	12
	3	AVS	2	14
	4	Pitfall or BVS	1	15

terms. The scheme generated for the mean number of species and individuals is quite similar (Fig. 2). There is not a significant between-habitat variation in the number of individuals or species collected by pitfall-traps, BVS or beating. The AVS method collected a significantly greater number of species and individuals in shrub and grassland than in forest (Fig. 2), only in the grasslands did it capture more species and individuals than BVS and pitfall traps; its captures equalled those of beating in the three habitats. Likewise, sweeping method captures also varied with habitat; the mean number of species and individuals captured in grasslands was significantly smaller than in the other two habitats (Fig. 2). Indeed, the sweeping method captured more species and individuals in forest and shrub, while in grassland its performance was similar to that of beating or AVS.

DISCUSSION

Methods differ greatly in the number of species and individuals caught, and collecting method performance depends on vegetation structure. Sweeping is a standard item in an arachnologists fieldwork due to its ease of use and effectiveness (Buffington & Redak 1998). It was the most efficient sampling method in forest and shrub sampling plots, and sweeping yielded more species and individuals. However, in the grassland sampling plot, the extreme shortness of the grass and the presence of thorny shrub patches limited its use; AVS and beating there produced equal value of mean individuals and species richness. While other authors have also noticed the reduced usefulness of sweeping in certain habitats (Churchill & Arthur 1999), as sweeping was found here to yield unique species in the three sampling plots, it must continue to be fundamental to sampling protocol.

Because beating and AVS work on similar vegetation habitats, they sample the same part of the spider community. However, while beating yielded unique species in the three habitats, AVS only did so in the grassland sampling plot, where araneids were concentrated in shrub patches and therefore easily spotted. Furthermore, AVS, a sampling method biased towards big and flashy spiders, yielded a greater proportion of araneids. It can be noticed that where vegetation structure makes visual search difficult, i.e. in the forest sampling plot, AVS is less efficient and beating yielded more (although not statiscally significant) species and individuals. Beating must be added to the sampling protocol, along with AVS in habitats with such a vegetation structure that the visual detection of individuals is easy.

Although its efficiency was quite low in our study, pitfall trapping, one of the most frequently used methods to sample surface-active terrestrial arthropod communities, is essential for sampling that part of the community (i.e., genera *Xysticus* and *Ozyptila*, which comprise more than the 70% of the Iberian thomisid fauna). Indeed, all the pitfall captures in the three sampling plots belong to these two genera. As already noted by other authors (Churchill 1993; Standen 2000), the captures of this sampling method were biased in favor of adult individuals, facilitating the identification of the specimens and helping in

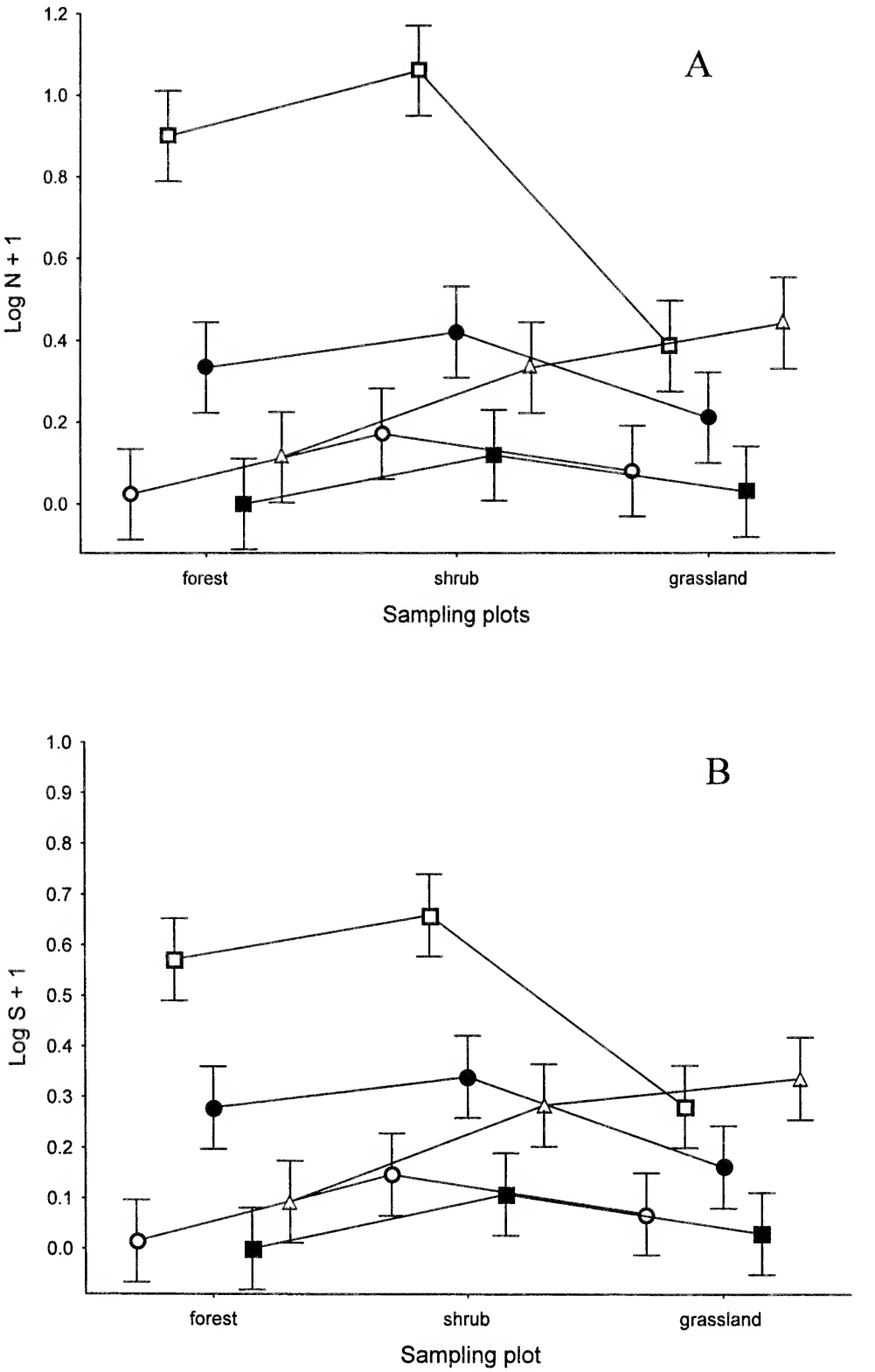

Figure 2.—Variation in the mean number of individuals (log of N + 1; ± 95% confidence interval) per sample (A) and mean number of species (log of S + 1; ± 95% confidence interval) per sample (B) between the three studied habitats or sampling plots. □ = sweeping; ● = beating; △ = AVS; ■ = BVS; ○ = pitfall trapping.

the inventory work. As BVS samples the same part of the community as pitfall traps do and does not contribute unique species, it can be done without. Thus, only pitfall trapping must be included in the sampling protocol.

Because the aim of this sampling protocol is the estimation of species richness, visual search could be more efficient if centered on new species, ignoring the common ones (Dobyns 1997; Churchill & Arthur 1999). The paucity of species and individuals captured by pitfall trapping suggests that the inventory would have been more effective if greater sampling effort were allocated to this method. Brennan et al. (1999) found that the larger the pitfall trap diameter, the greater the number of species captured. Work et al. (2002) pointed out that larger traps were more effective in the characterization of rare elements of an epigeal fauna. They also recommended combining large traps with smaller ones in order to sample a greater range of microhabitats. However, it is difficult to judge if the protocol would have been improved by changing the pitfall trap design or by trying another method that samples this epigeal fauna more accurately.

For none of the three sampling sites does the observed species accumulation curve reach an asymptote, although it seems that the simpler the vegetation structure, the smaller the curve-asymptote separation, and the smaller the difference between S_{obs} and the Clench model estimation from the nonparametric estimator values. Tight clustering of these three nonparametric estimators was also found by Toti et al. (2000), suggesting that they either estimate the same real value or are biased similarly. Other researchers working with the entire spider fauna (Coddington et al. 1996; Dobyns 1997; Toti et al. 2000; Sørensen et al. 2002) have also failed to produce asymptotic species accumulation curves. However, according to the estimations obtained, the three inventories sampled around 80% of spider fauna, indicating that it is possible to estimate the probable number of species in a 1 km^2 plot. The percentages of completeness are quite similar to those found by other authors in temperate forests (Dobyns 1997, 89%; Sørensen et al. 2002, 86–89%).

Our study is just a spring "snapshot" of the entire annual spider species richness of three sampling plots in different habitats. Spider assemblages, dynamic during the season, change in species composition. Thus, results depend on the time of sampling (Churchill & Arthur 1999; Riecken 1999). Nevertheless, estimating species richness accurately at a given time carries weight because sampling designs for annual studies depend on it (Coddington et al. 1996; Sørensen et al. 2002). Determining the proportion of the entire annual spider fauna that is represented in the spring sample is an objective of work currently being carried out.

Spider life history and behavioral diversity pose a challenge to the development of a precise and cost-effective sampling program (Costello & Daane 1997). Studies that have tried to take in the entire range of spider fauna have found that even intensive sampling does not reflect the whole of species richness (Coddington et al. 1996; Toti et al. 2000; Sørensen et al. 2002). So, Sørensen et al. (2002) suggest that long-term monitoring programs should focus on single, or few, families, or a single feeding guild, and use a few standardized and practical sampling methods. Our study has focused on two abundant spider families, Araneidae and Thomisidae, and has shown that a particular combination of sampling methods in each habitat is required to optimize efficacy and minimize effort. Sweeping, beating, pitfall traps and AVS in specific locations yield a reliable inventory of these two spider taxa in a 1 km^2 plot. Given how imperative a more detailed knowledge of Iberian spiders is, additional studies should be carried out in order to develop standardized sampling protocols for other spider families and/or guilds.

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SURFACE ULTRASTRUCTURE OF LABIAL AND MAXILLARY CUSPULES IN EIGHT SPECIES OF THERAPHOSIDAE (ARANEAE)

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ABSTRACT. Surface ultrastructure of labial and maxillary cuspules was studied in eight species of seven different genera of Theraphosidae. Cuspule ornamentation was observed through SEM images and comparisons were made among labial and maxillary cuspules of different species and different zones of each cuspule. Ornamentation patterns were different on the anterior face of the cuspule with respect to the posterior face. A significant correlation analysis between cuspule size and body size was found. The systematic use and the probable functions of the cuspules are discussed.

Keywords: Oral cuspules, cuspule ultrastructure, theraphosids

Labial and maxillary cuspules are globular to conical sclerotized features on the inner ventral corner of the maxillae and on the median-anterior side of the labium. They are exclusively found in mygalomorph spiders (Raven 1980, 1985). The number and distribution of cuspules has been used in mygalomorph systematics by several authors including Raven (1978, 1980, 1985, 1994), Griswold (1985), Snazell & Allison (1989), Goloboff (1993), Griswold & Ledford (2001), Pérez-Miles (1992, 2000) and Pérez-Miles et al. (1996), but studies on cuspule microstructure are scarce. Maxillary cuspule microstructure has been studied in Microstigmatidae (Griswold 1985), Barychelidae (Raven 1994) and in the theraphosid *Aphonopelma seemanni* (F.O.P.-Cambridge 1897) by Cutler & Vuilliomenet (2001). There are no explicit descriptions of the microstructure of labial cuspules although Raven (1994) suggested that they are similar to maxillary ones. In the present study, the surface ultrastructure of labial and maxillary cuspules were examined by SEM in eight theraphosid species corresponding to seven different genera and three different subfamilies (Avicullariinae, Ischnocolinae and Theraphosinae). This is a first approach to test the systematic value of such features in Theraphosidae. The possible mechanical, glandular and sensorial functions of the cuspules are discussed.

METHODS

Males of eight theraphosid species representing three subfamilies were studied including the Avicullariinae: *Iridopelma hirsutum* Pocock 1901; the Ischnocolinae: *Oligoxystre argentinense* (Mello-Leitão 1941) and the Theraphosinae: *Acanthoscurria suina* Pocock 1903, *Eupalaestrus weijenberghi* (Thorell 1894), *Grammostola iheringi* (Keyserling 1891), *Grammostola mollicoma* (Ausserer 1875), *Homoeomma uruguayense* (Mello-Leitão 1946), *Plesiopelma longisternale* (Schiapelli & Gerschman 1942). Seven individuals of *A. suina* and five of *E. weijenberghi* were additionally studied to estimate intraspecific variation. Body size was estimated from the carapace length of each individual measured dorsally with an ocular micrometer. One maxilla and the labium of each individual were removed for the observation of cuspules in a scanning electron microscope (SEM). Cuspule maximum width was measured from SEM images. Cuspules were counted using a stereoscopic microscope with an ocular reticule in fields of 1 mm^2 taken randomly from the labium and maxilla with at least 6 fields counted from each piece. Mean cuspule density was used as an estimator of the total number of cuspules. Nonparametric correlations were done using Spearman R test, means were compared by the Student's t test with restrictions for the variance. All individuals studied, including voucher specimens, were deposited

in the Arachnological collection of the Facultad de Ciencias, Montevideo, Uruguay.

RESULTS

Shape, size and density.—Cuspules are placed in groups on the anterior median zone of the labium and on the inner ventral corner of the maxillae (Figs. 1–7). They are implanted approximately perpendicular with respect to body surface (venter of labium and maxillae). Labial and maxillary cuspules are similar (Figs. 8–11), globular-conical, short or more elongated, thick and reddish brown. Some cuspules showed a slight constriction in the middle of their length. Two faces could be recognized: anterior (oral, Fig. 8) and posterior (Fig. 9). Cuspules are inserted in circular sockets where the anterior edge is higher than the posterior edge (Fig. 9). General shape shows a similar pattern in most species with only slight differences (Figs. 8–23). No pores were found on the cuspule surface on any of the species studied. Cuspule size ranged from 39.6–107.8μm Table 1. A significant correlation between cuspule maximum diameter and body size was found in the labium ($r = 0.89$; $P < 0.05$) and also in the maxillae ($r = 0.97$; $P < 0.05$). We did not find significant correlation between body size and the number of labial and maxillary cuspules ($r = -0.60$, $P = 0.48$; $r = -0.32$, $P = 0.48$, respectively).

Intra-specific variation in cuspule width was less than 10% in *A. suina* (mean 46.01 ± 3.46 SD, $n = 7$) and in *E. weijenberghi* (mean 50.7 ± 3.22 SD, $n = 5$) and no significant differences were found between sexes in these species ($t = 1.017$, $P > 0.30$; $t = 0.246$, $P > 0.80$, respectively). We found significant differences in cuspule width between these species ($t = 3.52$, $P < 0.01$).

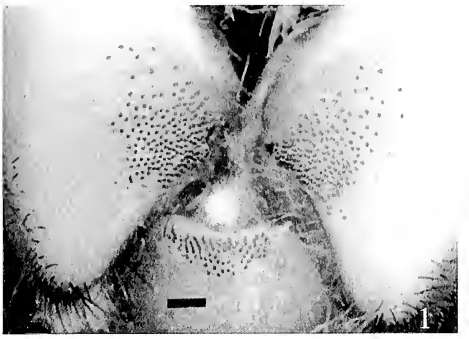
Cuspule ornamentation.—The surface of the labial cuspules is completely covered by ridges. The general pattern of ridges resembles the shape of a finger print in most species. Ornamentation of the anterior face differs from the posterior face. The disposition of ridges also differs in different zones of each face, comparing basal, median and apical zones. The general morphology and ornamentation of the cuspule is similar in all species studied, with the exception of dimensions. Slight variations among cuspule morphology and ornamentation in the same individual are similar to intra-specific and interspecific variations in the species studied.

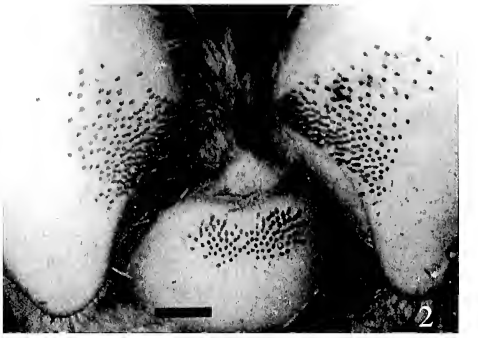
In a general pattern, the anterior face (Figs. 8, 10, 12, 14, 16, 18, 22) has parallel longitudinal ridges on the basal half and parallel transverse ridges on the apical half (which are continued by the circular ridges in the posterior face). In this face the longitudinal ridges are fused to the transversal ridges in several points of contact. The posterior face of the cuspules show longitudinal and diagonal ridges in the basal half; the central zone shows small loose ridges that resemble a whirl or more or less parallel ridges (Figs. 9, 11, 13, 15, 17, 19, 20, 21, 23). The periphery of the apical zone has circular to oval concentric parallel ridges. The intra-specific study shown that in *A. suina*, the interdistances between two ridges were approximately 1.2 μm in labial cuspules and 1.7 μm ± 0.29 SD in maxillary cuspules. No significant differences were found in the interdistances between sexes ($t = 1.76$, $P > 0.10$). *Eupalaestrus weijenberghi* has both faces of cuspules similar to *A. suina*. The interdistances between two ridges were 1.2 μm in labial cuspules and 1.6 μm ± 0.27 SD in maxillary cuspules. No significant differences were found in the interdistances between sexes ($t = 1.07$, $P > 0.30$). When we compared the interdistances of ridges between *A. suina* and *E. weijenberghi*, no significant differences were found ($t = 0.30$, $P > 0.70$).

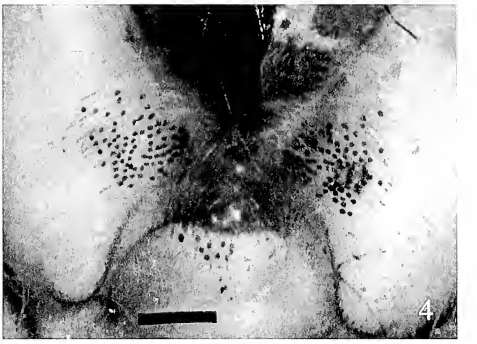
Interdistances between two ridges (in labial and maxillary cuspules respectively) in the other species studied were as follows: in *G. iheringhi* 2.4 μm and 1.8 μm; in *G. mollicoma* 2.3 μm and 2.5 μm; in *H. uruguayense* 1.3 μm and 1.5 μm; in *P. longisternale* 1 μm and 1.3 μm; in *I. hirsutum* 1.6 μm and 1 μm. *Oligoxystre argentinense* lacks labial cuspules, on coxal cuspules the interdistance between two ridges was 1.2 μm.

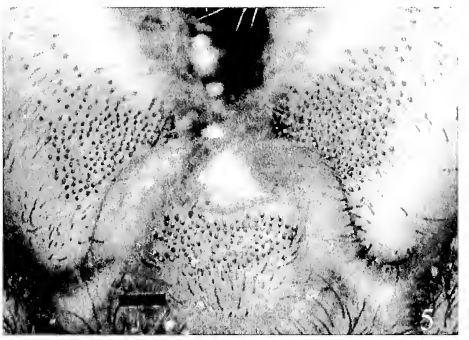
DISCUSSION

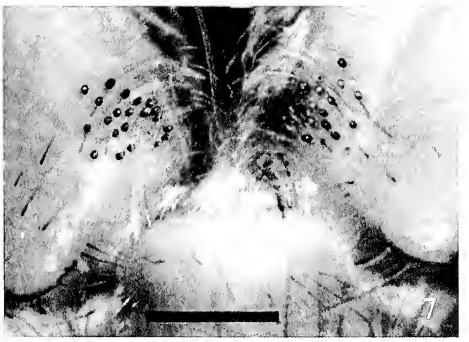
Raven (1994) found that maxillary cuspule size is independent on adult size in Barycheleidae. He found several discrete cuspule sizes related to the number of cuspules (in species with numerous cuspules, cuspules are small). In contrast, in the theraphosids studied, we found significant correlations between both maxillary and labial cuspule size with spider



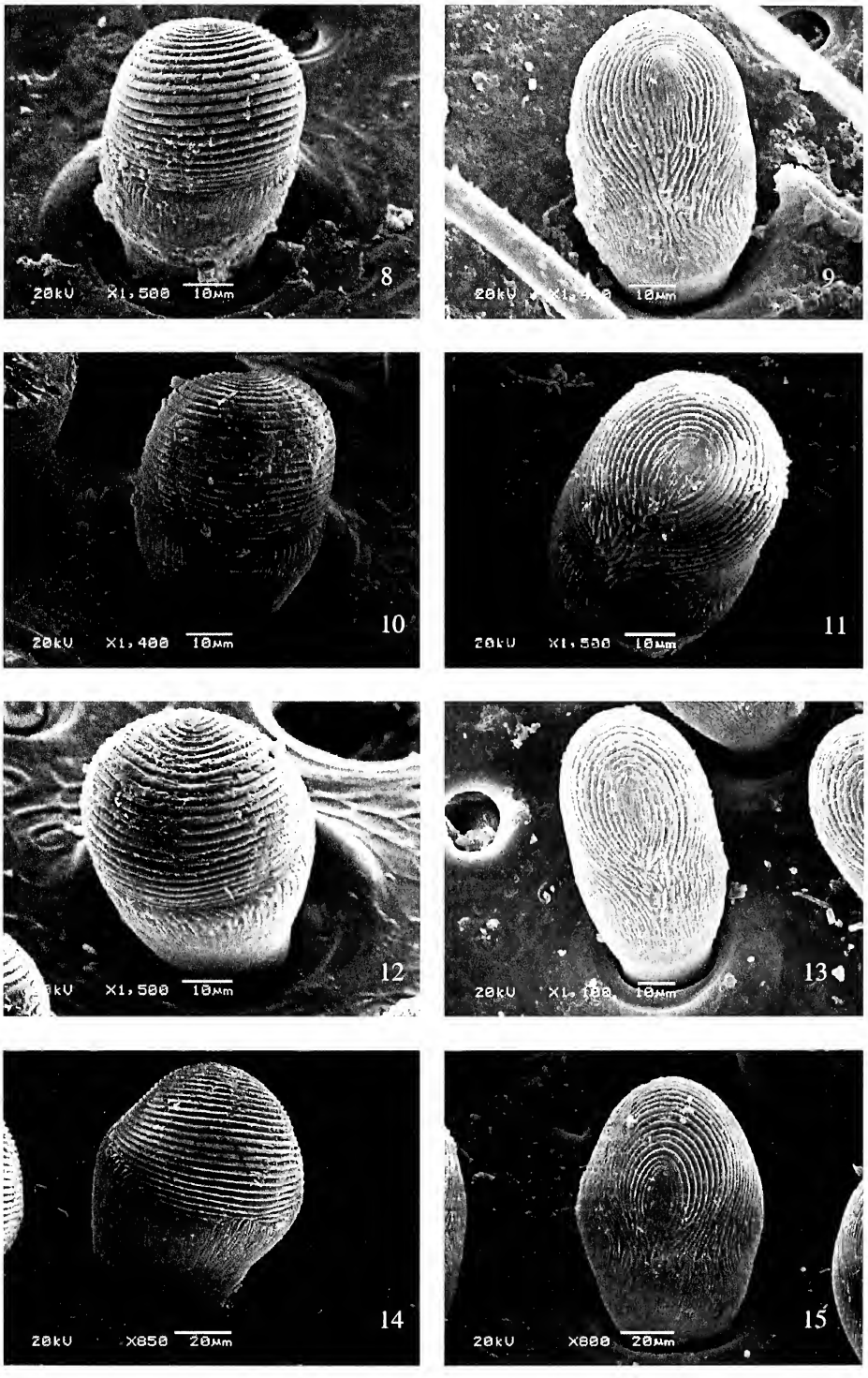








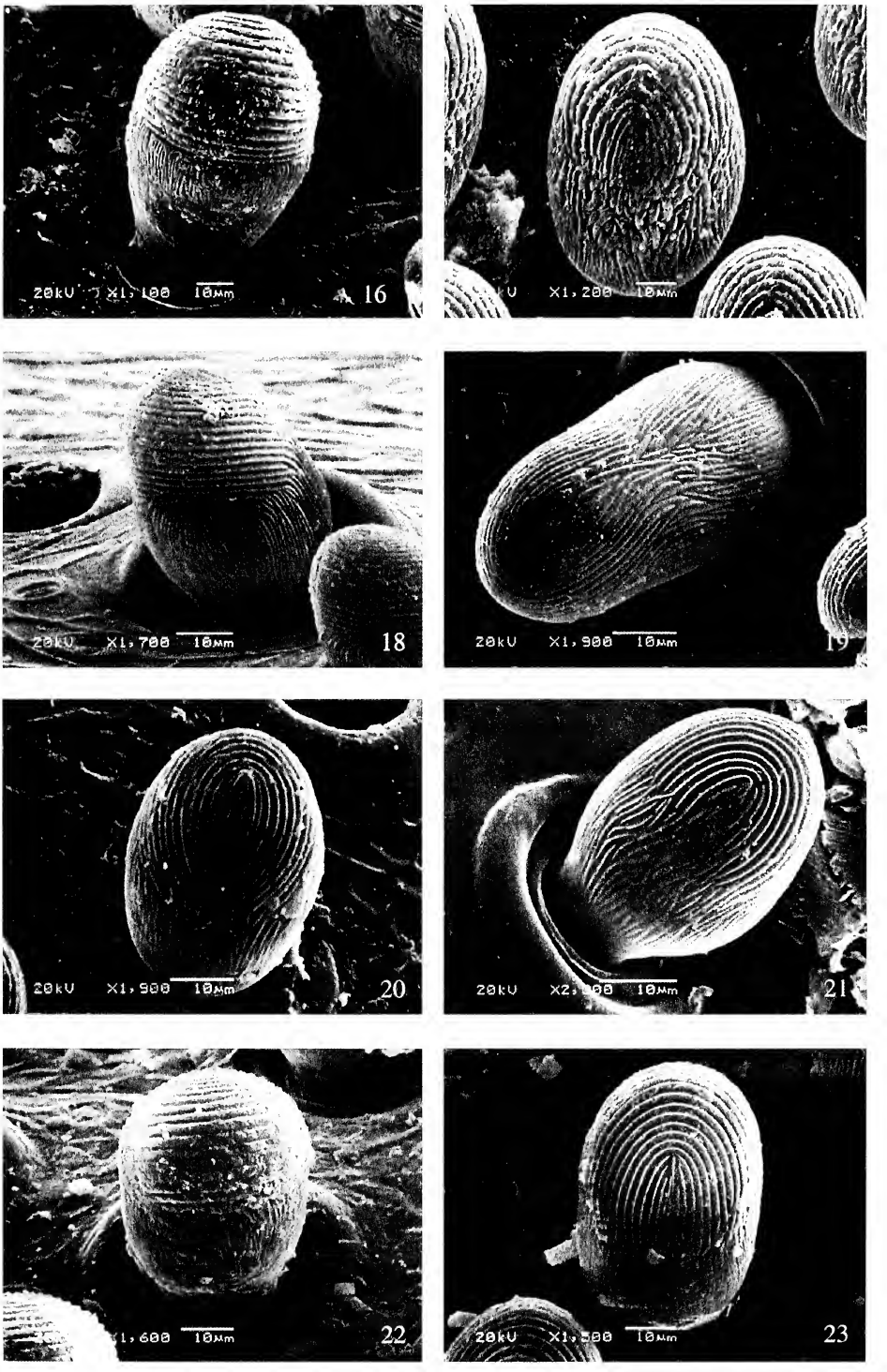
Figures 1–7.—Oral region of the species studied showing position of maxillary and labial cuspules. 1. *Acanthoscurria suina*. 2. *Eupalaestrus weijenberghi*. 3. *Grammostola mollicoma*. 4. *Homoeomma uruguayense*. 5. *Plesiopelma longisternale*. 6. *Iridopelma hirsutum*. 7. *Oligoxystre argentinense*. (Scale = 0.5 mm).



Figures 8–11.—Cuspules of *Acanthoscurria suina* male. 8, 9. Maxillary cuspules. 8. Anterior view. 9. Posterior view. 10, 11. Labial cuspules. 10. Anterior view. 11. Posterior view.

Figures 12–13.—Maxillary cuspule of *Eupalaestrus weijenberghi*. 12. Anterior view. 13. Posterior view.

Figures 14–15.—Labial cuspule of *Grammostola iheringi*. 14. Anterior view. 15. Posterior ventral view.



Figures 16–17.—Maxillary cuspule of *Grammostola mollicoma*. 16. Anterior view. 17. Posterior view.
Figures 18–19.—Labial cuspule of *Plesiopelma longisternale*. 18. Anterior view. 19. Posterior view.
Figure 20.—Labial cuspule of *Homoeomma uruguayense*, posterior view.
Figure 21.—Maxillary cuspule of *Oligoxystre argentinense*, posterior view.
Figures 22–23.—Labial cuspule of *Iridopelma hirsutum*. 22. Anterior view. 23. Posterior view.

Table 1.—Sizes (single cuspules) and density of cuspules in eight species of theraphosid spiders.

Taxa	Length (μm)		Width (μm)		Density of cuspules (number/mm²)		Density of ridges (number/10μm)	
	Labial	Maxillary	Labial	Maxillary	Labial	Maxillary	Labial	Maxillary
Theraphosinae								
Acanthoscurria suina	58.3	61.3	40.8	38.7	3.0 ± 1.5	4.0 ± 4.2	9	7
Eupalaestrus weijenberghi	71.2	74.3	41.5	39.3	3.8 ± 1.8	6.3 ± 3.9	7–9	10
Grammostola iheringi	98.5	107.8	70.2	69.8	4.5 ± 1.3	4.5 ± 1.1	6	6
Grammostola mollicoma	74.1	72.5	46.2	50.0	2.2 ± 0.9	2.7 ± 1.6	5	5
Homoeomma uruguayense	43.0	40.9	31.1	28.5	7.0 ± 4.3	6.0 ± 4.2	9	10
Plesiopelma longisternale	53.8	71.3	29.1	38.0	10.7 ± 3.0	7.7 ± 7.0	11	8
Aviculariinae								
Iridopelma hirsutum	53.7	69.7	36.8	33.9	4.5 ± 2.3	4.9 ± 3.2	7	13
Ischnocolinae								
Oligoxystre argentinense	—	39.6	—	27.8	—	4.8 ± 1.7	—	10

size. No significant correlation was found between cuspule number and cuspule size.

Two models of ornamentation were described in the maxillary cuspules of the Microstigmatidae (Griswold 1985): one presenting deep grooves and the other with many fine shallow grooves, the former considered as synapomorphic of clade "c" of Griswold (1985). Raven (1994) suggested the study of cuspule ridge interdistances (0.5–1 μm or 3–5 μm) to distinguish between two patterns in Nemesiidae. The interdistances of cuspule ridges found in the theraphosid species studied have intermediate values (0.9–2.5 μm) between Raven's groups and their aspect fits with Griswold's (1985) second model ("many fine shallow groves").

The differences in ornamentation found between the anterior and the posterior faces of the cuspules is here reported for the first time in Theraphosidae. However, these differences in ornamentation are probably also present in Microstigmatidae and Barychelidae considering the figures given by Griswold (1985:6, figs. 17–18) and Raven (1994:303–310, figs. 3–10) respectively. A unique cuspule description from a theraphosid species was done by Cutler & Vuilliomenet (2001) in *Aphonopelma seemani*. In our opinion this description corresponds to the posterior face.

No strong differences were found in cuspule morphology or ornamentation among the genera and species studied. This, together with the similarity in other families, could reflect that cuspules are an early synapomorphy at the level of the Mygalomorphae as was indicated by Raven (1980) and could be interpreted as a conserved feature through the evolution of several mygalomorph taxa. We therefore suggest these structures have limited systematic value.

The probable functions of the cuspules in theraphosids could be mechanical, sensorial and glandular. Cutler & Vuilliomenet (2001) suggest a glandular or sensory function for the cuspules of *A. seemani* on the basis of a pore observed on the apical region of the cuspules, that could be interpreted as a sensory pit or secretory gland. We did not observe any pore on labial nor maxillary cuspules. Considering the oral inclination of the cuspules, their ornamentation and their unique presence in my-

galomorphs with paraxial chelicerae, a mechanical function seems probable. Cuspules could help in prey retention by opposing the backward force of the chelicerae. The ornamentation of the apical half of the anterior face with transverse ridges could be related to particle retention near the mouth.

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NATURAL HISTORY AND KARYOTYPE OF SOME ANT-EATING ZODARIID SPIDERS (ARANEAE, ZODARIIDAE) FROM ISRAEL

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ABSTRACT. Natural history, including phenology, circadian activity, mimicry, reproduction, prey specialization and karyotype was studied in the zodariid spiders *Trygettus sexoculatus*, *Zodarion cyrenaicum*, *Z. lutipes* and *Z. nitidum* (Zodariidae, Zodariinae) found in Israel. The spiders were active throughout the year, with maximum seasonal activity in the summer. Two distinct reproductive periods were found for *Z. cyrenaicum* and *Z. nitidum*, one in May and the other in November. Individuals of all species studied were observed hunting only in the morning. Three zodariid species were found to generally mimic ants: *Trygettus sexoculatus* mimicked tiny yellow-brown ants such as *Monomorium niloticum*, *Z. cyrenaicum* mimicked large black ants such as *Messor arenarius*, and *Z. lutipes* mimicked large yellow-brown ants such as *Camponotus fellah*. The zodariids observed were able to subdue various ant species, from the subfamilies Formicinae, Myrmicinae and Dolichoderinae. *Trygettus sexoculatus* appeared to specialize on *Monomorium* sp., *Z. lutipes* on *Camponotus* sp. and *Z. cyrenaicum* on *Messor* sp. ants, i.e., the same ant species they imitate. When bitten by zodariids, Formicinae and Dolichoderinae ants were paralyzed much more quickly than Myrmicinae. Female zodariid paralyzed ants faster than juveniles and males. Courtship and mating were observed only in *Z. lutipes* and were found to be similar to other *Zodarion* species. The mean fecundity for all three *Zodarion* species ranged from 38–45 eggs per egg sac, thus being higher than reported in central European species. Females of all three species guarded egg sacs inside of their retreats. Karyotypes of studied *Zodarion* spiders were similar to the karyotypes of other zodariid spiders in terms of the diploid number (26 in *Z. cyrenaicum* and 25 in both *Z. lutipes* and *Z. nitidum*), sex chromosome systems and morphology of chromosomes. Most of the data indicate that the *Zodarion* species of this study have a close affinity to a group of Western European *Zodarion* species.

Keywords: Myrmecophagy, specialization, mimicry, Formicidae, chromosomes

The family Zodariidae is a species rich group of spiders, which includes more than 570 species in six subfamilies with worldwide distribution, but is most abundant in the subtropical region (Platnick 2002). Zodariid spiders were neglected on a worldwide scale until recently, when Jocqué (1991) produced a generic revision. Very little information is reported on the natural history of zodariid spiders (e.g. Wiehle 1928; Harkness 1976; Cushing & Santangelo 2002).

In the Mediterranean region, representatives of two subfamilies and more than 110 species have been found. The majority of species belong to the most advanced subfamily, Zodariinae. The diversity of this subfamily seems to decline from west to east in the Mediterranean region. In the western and the central area, three genera and about 60 species of Zodariinae were found and in the eastern part five genera with only about 30 species. This may be explained, in part, by the lack of collecting in the eastern region. In fact, in the eastern Mediterranean only the zodariid spiders of Israel have been revised so far. Altogether 13 species of the genera *Palaestina*,

Ranops, *Trygettus* and *Zodarion* were reported from Israel (Levy 1992).

In spite of the lower number of species in the eastern Mediterranean, the zodariid fauna of Israel shows a remarkable diversity perhaps due to the fact that Israel is situated where two biogeographic regions, the Palearctic and the Ethiopian, meet. However, little is known of the natural history of these zodariid spiders. The purpose of this study was to gather data on the natural history and karyotypes of the four most abundant species, *Trygettus sexoculatus* (O.P.-Cambridge 1872), *Zodarion cyrenaicum* Denis 1935, *Zodarion lutipes* (O.P.-Cambridge 1872), and *Zodarion nitidum* (Audouin 1826) and to compare them to the European *Zodarion* species that have been studied (Couvreur 1990a; Pekár & Král 2001). This study contributes to the understanding of the adaptive radiation within Zodariinae and particularly within the genus *Zodarion*. Members of the subfamily Zodariinae are remarkable for their diet specialization on some social insects (ants and termites) and for the frequent occurrence of ant mimicry. Information on phenology, diet specialization and mimicry as well as the number and morphology of their chromosomes was compared with similar data reported for the European species (Pekár & Král 2001).

Trygettus sexoculatus, *Z. cyrenaicum*, and *Z. nitidum* are found in Israel and in North Africa; *Z. lutipes* occurs in Crete and north of Israel, in Lebanon and Turkey (Levy 1992). In Israel, *T. sexoculatus* occurs in the central and southern arid region. *Zodarion nitidum*, a desert spider, occurs mainly in the Negev desert. *Zodarion lutipes* was found only as far south as the north-western part of the Negev desert (desert edge). *Zodarion cyrenaicum* occurs in the northern part of the Negev desert. It is occasionally sympatric with *Z. nitidum* in the desert, while in the northern Negev it occurs syntopically with *Z. lutipes* (Fig. 1).

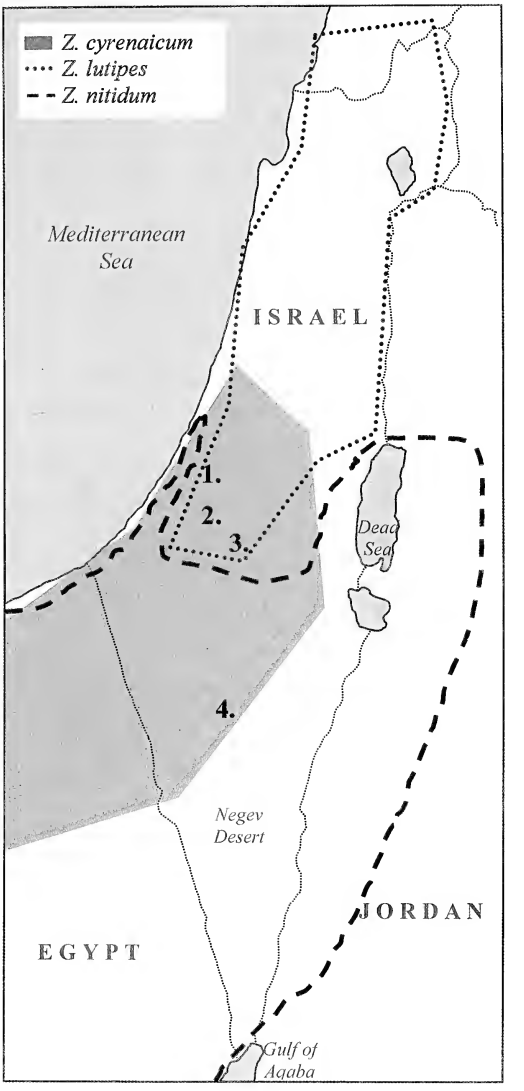


Figure 1.—The distribution of *Zodarion* species in Israel reported in this study. Sites mentioned in the text are indicated: 1. Be'eri Nature Reserve, 2. Fura Nature Reserve, 3. Lehavim, 4. Sede Boqer.

METHODS

Study areas.—Numerous specimens of *Z. cyrenaicum* and *Z. lutipes* were collected in the weedy margin of a melon field at the Bitronot-Be'eri Nature Reserve (about 40 km NW of Be'er Sheva, 31°26′N, 34°29′E). These two species, together with *T. sexoculatus*, were collected and observed also on an open slope of a semi-desert steppe character close to Lehavim, at the northern edge of the Negev desert (about 10 km NE of Be'er Sheva, 31°22′N, 34°48′E). *Zodarion lutipes* was also found in Fura Reserve in semi-desert grassland habitat (about 20 km N of Be'er Sheva, 31°27′N, 34°45′E). *Zodarion nitidum* was very abundant in a large-scale spider diversity project of the Negev desert that began in the early 1990's (Pekár & Lubin 2003). However, in March & April 2001 a three-week intensive search for these spiders in the surroundings of Sede Boqer (Haluqim Ridge, 30°51′N

34°45′E) yielded only five specimens. Boeken et al. (2001) noted that a severe drought in 1999 followed by drought in 2000 caused a dramatic decline of plant density in the Negev. It is likely that these droughts considerably reduced the population density of *Zodarion* species.

Material and analyses.—Data used to extrapolate the seasonal activity and phenology of zodariids came from the large-scale project on the diversity of spiders of the Negev desert (Proszyński & Lubin 1994; Pekár & Lubin 2003). Spiders were sampled at 45 sites in the Negev between September 1990 and July 1993. The spiders were collected using pitfall traps that were opened for 3 consecutive days each month. No preservative was used in the traps (diameter and depth 10 cm) and the spiders were collected each morning. Immature *Zodarion* individuals were identified to species based on the color.

Circadian activity of spiders was observed in 2001 as the number of spiders found during 5 min in the vicinity of ant nests or along ant trails (in the case of *Messor* ants). As the sites in the northern Negev were not easily accessible, the activity of spiders was observed only during the day, between 0900 and 1900. At Sede Boqer, the activity of ants was observed for 24 hours on one day in the beginning of April. On that day the sunrise was at 0530 and the sunset at 1800. Activity of four ant species (the most frequent in the study sites), namely *Camponotus fellah* Dalla Torre 1893, *Cataglyphis albicans* (Roger 1859), *Messor arenarius* (Fabricius 1787) and *Monomorium niloticum* Emery 1881, was estimated every hour as the number of ants counted per 15 s at four nest entrances.

The behavior of the different species was investigated in the laboratory. Twenty-seven individuals of *Z. cyrenaicum*, 21 of *Z. lutipes*, 10 of *Z. nitidum* and four of *T. sexoculatus* were brought to the laboratory. Spiders were kept singly in glass tubes (60 x 15 mm) in a constant temperature 25 ± 2 °C and L:D = 14:10 and were fed twice a week with various ant species. To observe courtship and mating, adult males were introduced into tubes occupied by females. After mating the males were separated from the females. The number of egg sacs produced and the fecundity (total number of eggs) were recorded.

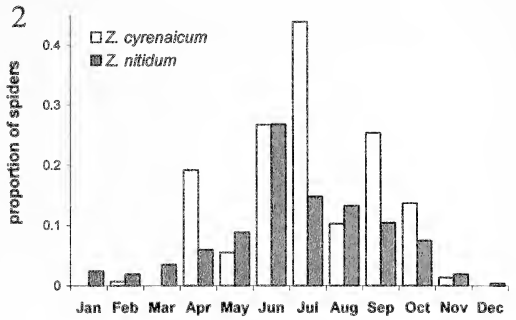
In the feeding experiments spiders were put singly to a Petri dish (diameter 40 mm, with a filter paper attached to the bottom) a day before the experiment started. Ten individuals of each *Zodarion* species and four specimens of *Trygettus* were used. Four ant species, namely *C. albicans* (Formicinae), *M. arenarius*, *M. niloticum* (Myrmicinae) and *Tapinoma simrothi* Krausse 1911 (Dolichoderinae), were offered to each individual of *Zodarion* species. Three ant species, *Pheidole pallidula* Nylander 1849, *M. niloticum* (Myrmicinae) and *T. simrothi* (Dolichoderinae), were offered to *T. sexoculatus*. The ants were offered to spiders randomly over a 4 day interval. All ants were weighed before the experiment. *Cataglyphis* and *Messor* ants were disabled by removing the distal parts of mandibles before the experiments. Other ant species were not disabled. An ant was released into a dish occupied by a spider; if the spider did not attack the ant within 15 min the experiment was terminated. Latency to the first attack, number of attacks and the paralysis latency (time to paralyze the ant) were observed for each trial. The latency to the first attack was estimated as the time from the first encounter between spider and ant to the first attack. The paralysis latency was estimated as the time between the first attack and complete immobilization, i.e. when an ant could not raise itself after being touched with forceps.

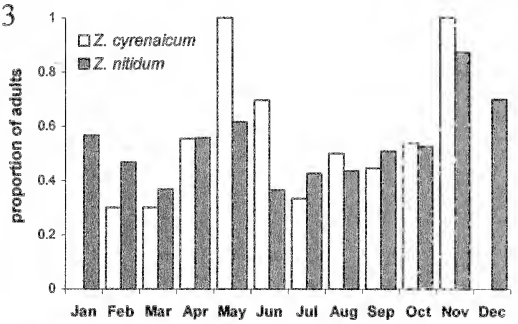
Data were analyzed using Generalized Linear Models (GLM) in Statistica (StatSoft 2001). The body mass of an ant was expected to have an effect on the number of attacks and on paralysis latency, therefore ant mass was first regressed (using linear regression) on these dependent variables. However, ant mass had no effect on the number of attacks and therefore could be ignored in the analyses. As the data followed a Poisson error structure, a log-linear analysis was used with three factors (see below). Over-dispersion was resolved by adjusting the scale parameter. The same method was used to analyze data on the latency to the first attack. The paralysis latency was affected by ant body mass, which was set as a covariate. The paralysis latency data were log transformed and further analyzed using ANCOVA. In all analyses the factors were (1) *Zodarion* species (*Z. cyrenaicum*, *Z. lutipes*, and *Z. nitidum*), (2) developmental stage or sex of spider (female, male, and juvenile) and (3) ant subfamily (Dolichoderinae, Formicinae

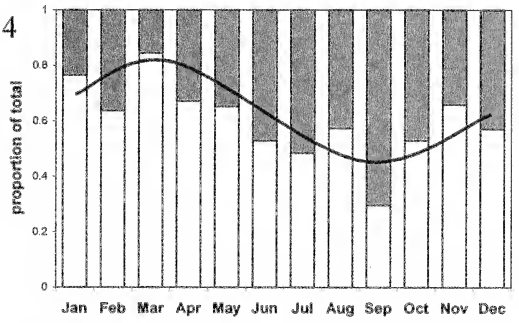
and Myrmicinae). Post-hoc comparisons were made using Tukey's HSD test.

For the karyological analyses three individuals of *Z. cyrenaicum* (locality Bitronot-Be'eri), five individuals of *Z. lutipes* (Lehavim), and 12 individuals (reared from two egg sacs) of *Z. nitidum* (Hatira), representing both sexes and various developmental stages, were used. However, only the testes of subadult males (two in *Z. cyrenaicum*, three both in *Z. lutipes* and *Z. nitidum*) gave interpretable chromosomal figures. The chromosome preparations were obtained by a modification of the spreading technique used by Traut (1976). The gonads were dissected from the abdomen in a hypotonic solution (0.075M KCl) and moved to fresh hypotonic solution so that the tissue was hypotonized for 10 min in total. This was followed by 10 min fixation in freshly prepared Carnoy fixative (ethanol: chloroform: glacial acetic acid 6:3:1) and 25 min fixation in a new Carnoy fixative. Afterwards, the tissue was placed in a drop of 60% acetic acid on a clean slide and quickly shredded as finely as possible with a pair of fine tungsten needles. The slide was quickly moved onto a warm histological plate (surface temperature of 40 °C) and the drop of dispersed tissue was allowed to evaporate while moving it constantly using a fine tungsten needle. Slides were air-dried at room temperature overnight and stained with 5% Giemsa solution in Sörensen phosphate buffer (pH = 6.8) for 25–30 min (Cokendolpher & Brown 1985).

Zodariid spiders were identified using Levy (1992) and ants were determined using an unpublished key of Kugler (1984). Voucher specimens of spiders and ants are deposited at the Department of Entomology of the Research Institute of Crop Production, Prague, the Czech Republic.



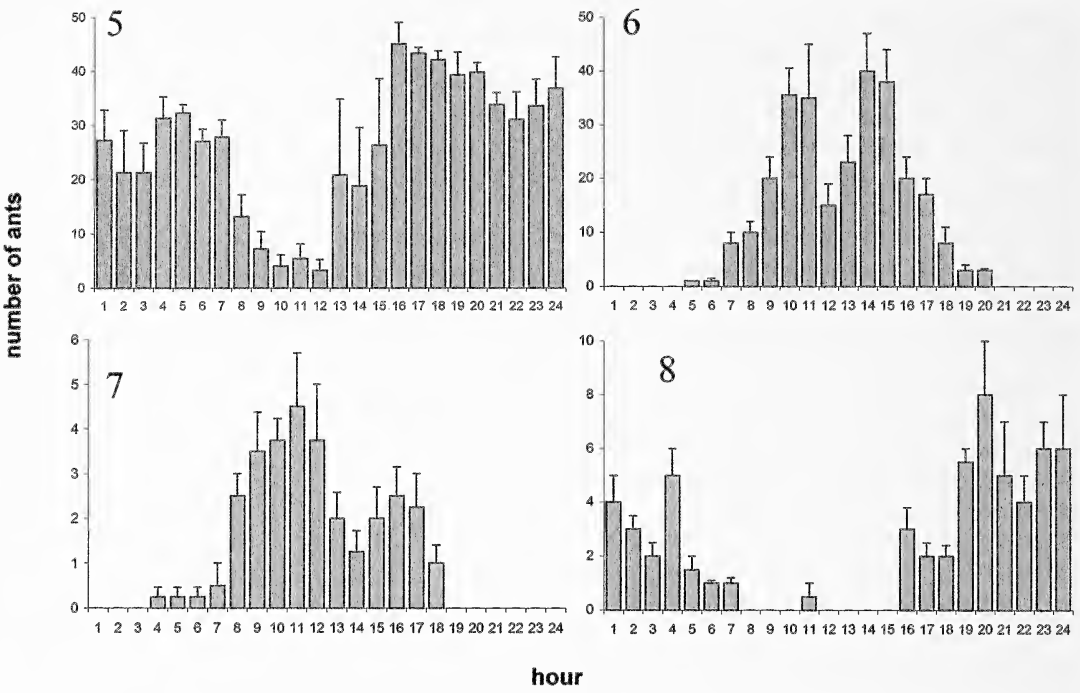




Figures 2–4.—Phenology of zodariid spiders collected in pitfall traps: data from three years (1991–3) combined. 2. Seasonal activity of *Z. cyrenaicum* and *Z. nitidum*, expressed as a monthly proportion. Total number of individuals: *Z. cyrenaicum* = 146, *Z. nitidum* = 2403. 3. Phenology of *Z. cyrenaicum* and *Z. nitidum* expressed as the proportion of adult spiders per month. 4. Monthly proportions of males (empty bars) and females (gray bars) of *Z. nitidum* with a polynomial curve.

RESULTS

Phenology.—Pitfall-trap sampling at regular intervals allowed us to outline the seasonal activity and phenology of *Z. cyrenaicum* and *Z. nitidum*. Data for *Z. lutipes* and *T. sexoculatus* were insufficient to determine any pattern. *Zodarion cyrenaicum* and *Z. nitidum* were active during the whole year (Fig. 2). The maximum seasonal activity (between 27–44 % of the total annual activity) of both species was in the summer months, June (*Z. nitidum*) and July (*Z. cyrenaicum*). There was minimal or no activity in the winter months, December (*Z. nitidum*) and January (*Z. cyrenaicum*). Adults of *Z. nitidum* were found throughout the year (Fig. 3), while no individuals of *Z. cyrenaicum* were trapped during the winter months. Both species had two reproductive peaks annually: spiders matured in spring (March) and autumn (November) and reproduced soon after. The proportion of males to females of *Z. nitidum* changed during

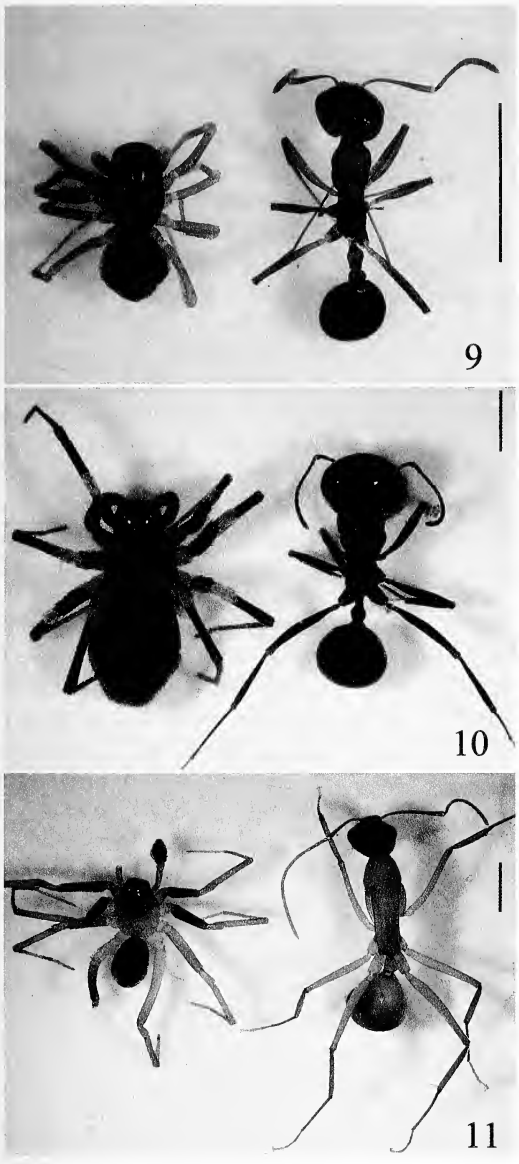


Figures 5–8.—Daily activity of ants expressed as number of ants recorded in 15 s: 5. *Messor arenarius*; 6. *Monomorium niloticum*; 7. *Cataglyphis albicans*; 8. *Camponotus fellah*. Bars represent mean + SE.

the year (Fig. 4). Whereas males dominated in spring (peak in March), females dominated in autumn (peak in September). In total the M/F ratio of individuals collected in pitfall traps was significantly skewed toward males 1/0.83 (binomial test, $P = 0.002$).

Activity.—*Zodarion* spiders were collected from igloo-shaped retreats underneath stones where they rest during the day. The retreats were made of sand pebbles or pieces of gastropod shells and were proportional to the size of the spider. In females the retreats were up to 2 cm in diameter. Individuals of *T. sexoculatus* were found under stones but never in a retreat. *Trygettus sexoculatus*, *Z. cyrenaicum* and *Z. lutipes* were active only in the morning, from 0900–1100, running among ants or hunting them. No *Z. nitidum* was observed at all during March–April 2001. In 2002, however, *Z. nitidum* was seen active in the morning hours (males and females) in the vicinity of nests of *M. arenarius* in sandy habitats. Activity of the four most abundant ant species, which are the prey of observed zodariid spiders, followed different patterns. *Messor* ants were active in the day as well as at night (Fig. 5), with a decline in activity between 0900 and 1400. *Monomorium* ants were active only during the day, from 0500–2000, with a decline at midday (Fig. 6). *Cataglyphis* ants were also active during the day only, from 0400–1800, with a slight decline between 1300 and 1400 (Fig. 7). *Camponotus* ants were active only from the afternoon (1600) and through the night until morning (0700; Fig. 8). The activity of ant species and of the spiders overlaps broadly.

Batesian mimicry.—Tentative ant models were found for three spider species. *Trygettus sexoculatus* imitates tiny yellowish-brown ants, especially *Monomorium niloticum*. Adult spiders are 2–2.5 mm in length, with yellowish prosoma and legs and the opisthosoma is dorsally dark brown with a glossy scutum (Fig. 9). Workers of *M. niloticum* are 3–3.5 mm in length with head, thorax, antennae and legs yellow to orange and the gaster dark brown. Adult spiders of *Z. cyrenaicum* mimic larger black ants, e.g. the small workers of *Messor arenarius*. The spiders are 3.5–8 mm in length with uniform blackish prosoma and opisthosoma. The legs are black, except for the coxae and patellae, which are pale (Fig. 10). Workers of *M. arenarius* are polymor-



Figures 9–11.—Spider mimics and their ant models. 9. *Trygettus sexoculatus* (female) and *Monomorium niloticum*; 10. *Zodarion cyrenaicum* (female) and *Messor arenarius*; 11. *Zodarion lutipes* (male) and *Camponotus fellah* (freshly hatched individual with light gaster). Scale lines = 2 mm.

phic, 4–15 mm and are uniformly black. Adult individuals of *Z. lutipes* resemble larger yellowish-brown ants, notably small workers of *Camponotus fellah*. The spiders are 3.5–6.5 mm in length, the prosoma is yellow with a brown cephalic part and the opisthosoma is dark brown (Fig. 11). All leg segments are yellow except for the first and second femora, which are brown. The model ants are 6–17 mm, with head and gaster dark brown while the thorax, antennae and legs are yellow to light brown. Individuals of *Z. nitidum* were observed with *M. arenarius* ants, which they do not appear to mimic closely.

Prey.—A few individuals were observed feeding on ants in the field. Four individuals of *Z. cyrenaicum* were observed feeding on *M. arenarius*, two individuals of *Z. lutipes* fed on *Messor semirufus* (André 1883) or *C. fellah* and three individuals of *T. sexoculatus* fed on *M. niloticum*. Feeding of *Z. nitidum* was not observed in the field. In laboratory experiments all *Zodarion* species were able to subdue larger ants of the genera *Cataglyphis* and *Messor*. Tiny ants were often ignored: only 24% (n = 30) of all *Zodarion* individuals attacked *M. niloticum* ants and 75% of *Z. cyrenaicum* and *Z. lutipes* (n = 20) attacked *T. simrothi* ants while no *Z. nitidum* attacked this ant. All *T. sexoculatus* (n = 4) attacked *M. niloticum* and *P. pallidula* but failed to catch *T. simrothi*. *Trygettus sexoculatus* always attacked ants only once while *Zodarion* spiders averaged two attacks per ant. There was no difference in the number of attacks on ants from different subfamilies, nor was there a difference between the *Zodarion* species. The latency to the first attack was significantly different for the three *Zodarion* species (GLM, P = 0.002). *Zodarion cyrenaicum* took almost four times longer to attack (119 s, SE = 46) than the other two species (30 s, SE = 5.1). There was also a difference between sexes and developmental stages (GLM, P = 0.0001). Males took about five times longer to attack (150 s, SE = 46) than females and juveniles (31.5 s, SE = 5.2). In *T. sexoculatus* the latency was on average 20 s (SE = 14.2). Myrmicinae ants attacked by *T. sexoculatus* were paralyzed on average after 3.1 min (SE = 0.34, n = 6) (Table 1). In *Zodarion* spiders the paralysis latency differed for developmental stages and species (Fig. 12). It was longest in males and shortest in females (GLM, P = 0.003). There was also a significant difference in paralysis latency between ant subfamilies (GLM, $P < 0.0001$). Myrmicinae ants were paralyzed on average after 64 min while Formicinae and Dolichoderinae after 17–19 min (Table 1). The three *Zodarion* species did not differ significantly in the paralysis latency for Myrmicinae. However, *Z. lutipes* paralyzed

Table 1.—Comparison of the number of attacks and the paralysis latency (min) on three ant subfamilies for three zodariid spiders. *Zodarion nitidum* did not attack dolichoderine ants, presumably because the spiders were large in comparison with the ants. *Trygettus sexoculatus* was not tested with formicine ants because the ants were too large for this species. All numbers are means ± SE.

Spider	Ant subfamily	No. of attacks	Paralysis latency
T. sexoculatus	Myrmicinae	1.0 ± 0.0	3.6 ± 0.13
	Dolichoderinae	0	—
Z. cyrenaicum	Formicinae	1.9 ± 0.4	26.7 ± 11.7
	Myrmicinae	2.2 ± 0.4	56.5 ± 11.1
	Dolichoderinae	2.1 ± 0.3	28.1 ± 15.3
Z. lutipes	Formicinae	2.2 ± 0.4	6.7 ± 1.4
	Myrmicinae	1.8 ± 0.2	71.2 ± 15.8
	Dolichoderinae	2.0 ± 0.7	3.5 ± 1.1
Z. nitidum	Formicinae	3.0 ± 0.6	19.0 ± 5.6
	Myrmicinae	2.4 ± 0.5	65.6 ± 11.7

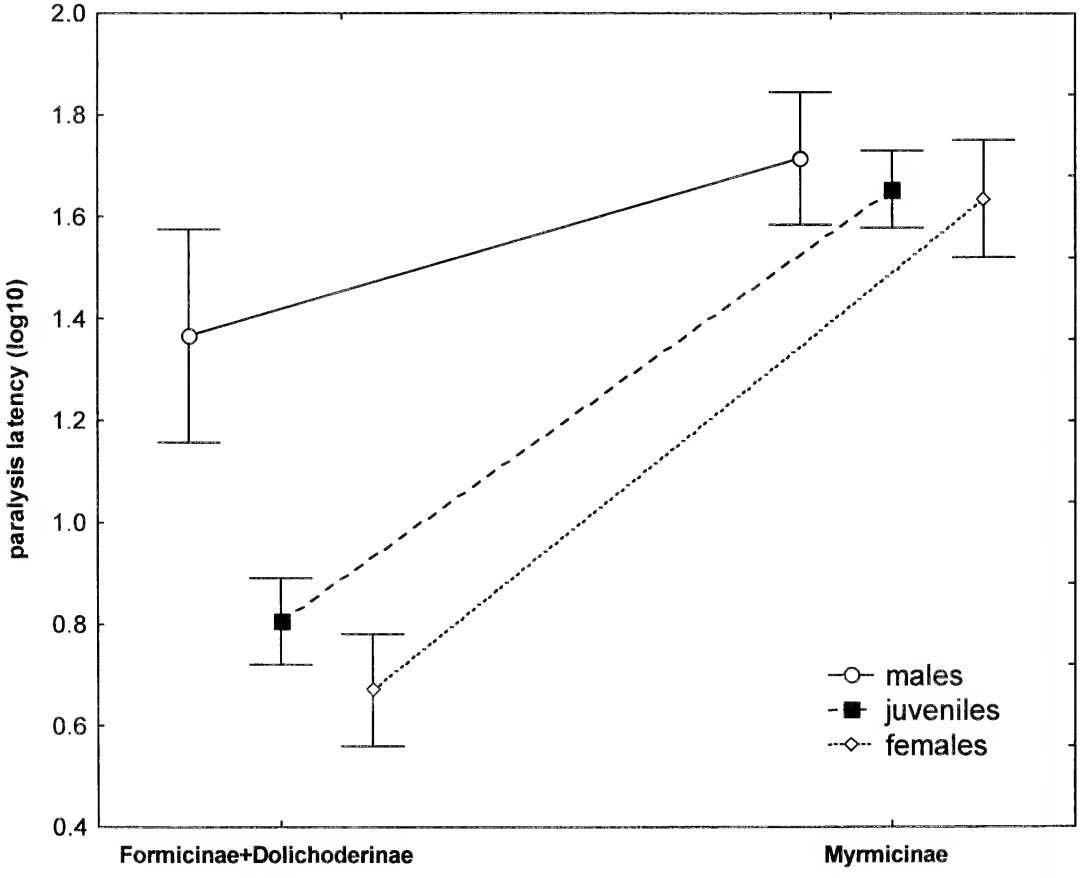


Figure 12.—Comparison of the mean (±SE) paralysis latency (min) for different *Zodarion* sexes and developmental stages (pooled for the three *Zodarion* species) and two ant subfamilies (Formicinae were pooled with Dolichoderinae).

Formicinae ants in a significantly shorter time than *Z. nitidum* and *Z. cyrenaicum* (Tukey HSD, $P = 0.0002$).

Enemies.—Of 73 collected specimens, only one subadult male of *Z. cyrenaicum*, collected from an igloo-shaped retreat in Lehavim, was found to have a larva of *Polysphincta* sp. (Hymenoptera, Ichneumonidae) attached to the anteriodorsal region of its abdomen. No other *Zodarion* spider in this study was found with a parasitoid wasp larvae and no other enemies were observed attacking *Zodarion*.

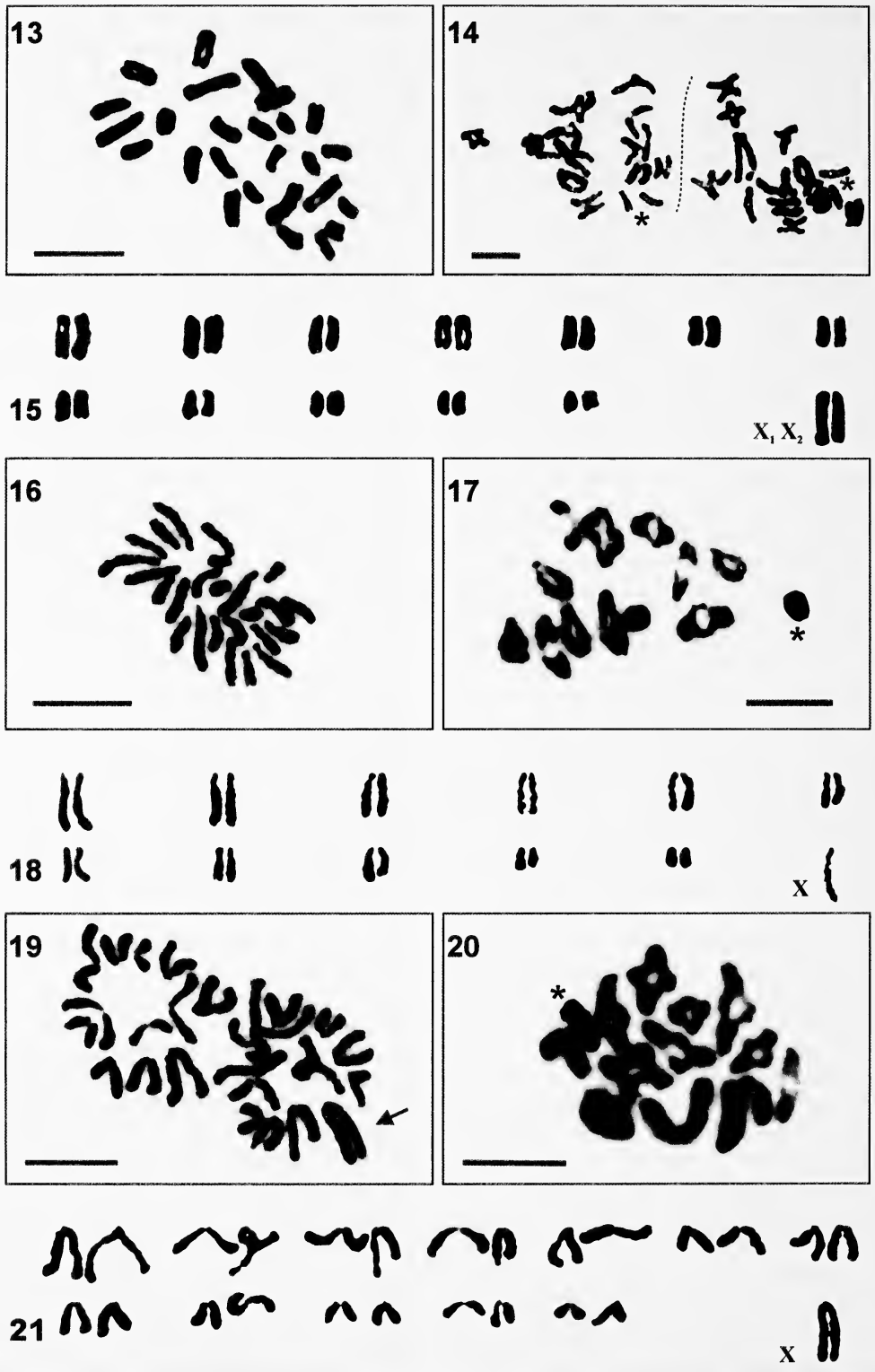
Reproduction.—Courtship was similar in all three *Zodarion* spiders. Males began to court after a brief contact with the female. The male slowly approached the female from the front with rapidly quivering forelegs, and touched her lightly. If the female was receptive she first responded by similar quivering of forelegs, then crouched and allowed the male to climb onto her and copulate. Copulation was observed only in *Z. lutipes*, lasting on average 1.58 min (SE = 0.5, $n = 5$). Males copulated from both sides inserting the appropriate palp, and interrupted several times. After each interruption males quivered the forelegs, otherwise the female would respond aggressively. In the other two *Zodarion* species only several attempted copulations (unsuccessful insertion of palpal organs) were observed, each lasting less than 10 s. Females of *Z. cyrenaicum* and *Z. lutipes* produced only one egg sac while females of *Z. nitidum* produced 1–3 egg sacs in captivity. Females of all species guarded the egg sac inside the retreat. A new egg sac was produced only after the previous one hatched. Mean fecundity in *Z. cyrenaicum* was 45 eggs/sac (SE = 7.5, $n = 5$), 39 eggs/sac (SE = 17.9, $n = 3$) in *Z. lutipes* and 38 eggs/sac (SE = 4.3, $n = 11$) in *Z. nitidum*. Spiderlings (pooled for all three *Zodarion* species, as there was no difference between species (ANOVA, $P = 0.22$)) hatched on average after 36.3 days (SE = 4.8, $n = 8$). No information on reproduction was obtained for *T. sexoculatus*.

Karyotype.—Both mitotic and meiotic phases were obtained from the testes of subadult males. The diploid chromosome numbers were as follows: *Z. cyrenaicum* 26 (Figs. 13, 15), *Z. lutipes* 25 (Figs. 16, 18), and *Z. nitidum* 25 (Figs. 19, 21). No individuals of *T. sexoculatus* were collected for karyological analysis. Karyotypes of all studied species were formed by acrocentric chromosomes exclusively. Chromosome pairs decrease gradually in size except for two shortest pairs in *Z. lutipes* (Fig. 18). Sex chromosome(s) of all species are among the longest chromosomes in the karyotype. Observation of sex chromosomes during meiotic division indicated an X_1X_20 sex chromosome system in *Z. cyrenaicum*. Sex chromosomes X_1 and X_2 were similar in size, the X_2 being somewhat shorter than X_1 (Fig. 14). *Zodarion lutipes* and *Z. nitidum* have an X0 sex chromosome system (Figs. 17, 20). The X chromosome of *Z. lutipes* and *Z. nitidum* exhibits positive heteropycnosis (greater condensation than autosomes) during the first meiotic division and interkinesis as well as in prophase II. Heteropycnosis of sex chromosomes in *Z. cyrenaicum* continues only to diplotene. However, weak heteropycnosis reappears also during interkinesis and prophase II. Sex chromosome(s) in males of all species lie on the periphery of meiotic figures until metaphase II.

DISCUSSION

Aspects of the biology of five species of the genus *Zodarion* have been reported (Couvreur 1990b; Harkness 1977; Pekár & Král 2001; Schneider 1971; Wiehle 1928), but only two central European species, *Z. germanicum* (C.L. Koch 1837) and *Z. rubidum* Simon 1914, have been studied in detail (Couvreur 1990b; Pekár & Král 2001). The latter authors found that these two species differ considerably from each other in their circadian activity, reproduction and karyotype.

The seasonal activity of the three *Zodarion* species studied here is similar to the central European species with greater activity in summer. Central European zodariid spiders are active from April to October. In the winter, between November and March, European species are inactive, obviously overwintering (Pekár & Král 2001) while the species studied in Israel have low activity levels throughout winter. Central European species are univoltine and stenochronous with one maturation period in June. Spiderlings hatch in July and reach adulthood the following year, 10–11 months after hatching (Couvreur 1990a; Pekár & Král 2001). Data on two species, *Z. cyrenaicum* and *Z. nitidum*, show that Israeli species are bivoltine and eurychronous, with two major maturation periods, one in spring and



Figures 13–21.—Karyotype of *Zodarion* males. 13–15. *Zodarion cyrenaicum*. 13. Mitotic metaphase. 14. Diplotene. 15. Karyogram. 16–18. *Zodarion lutipes*. 16. Mitotic metaphase. 17. Diplotene. 18. Karyogram. 19–21. *Zodarion nitidum*. 19. Metaphase of the second meiotic division. Arrow identifies X chromosome that differs from autosomes by closely aligned chromatids. 20. Diplotene. 21. Karyogram. Karyo-

the other in autumn. Data collected by Levy (1992) and data from this study suggest that *T. sexoculatus* and *Z. lutipes* have a similar phenological pattern. The tendency to multivoltinism is known also for other Mediterranean arthropods (so called "Mediterranean biotype"). For example, Bodenheimer (1943) found that populations of *Coccinella septempunctata* L. (Coleoptera) in Israel are bivoltine with one complete and one partial generation in spring and in autumn. Observations on the desert widow spider, *Latrodectus revivensis* Shulov 1948 (Theridiidae), indicate that this species has two peaks of maturation in Israel; a major one in spring and a minor one in autumn (Lubin et al. 1991). *Zodarion* species in Israel follow a similar pattern. It is not known how long it takes to complete one generation. Provided the development takes about six months there should be two non-overlapping generations in one year. If the development is about 10 months then there are two overlapping generations. For the spring generation it may be possible to mature in 6 months, i.e. by the end of summer, because ants are abundant and the temperature, controlling the rate of development, is sufficient. The autumn generation, however, might not be able to reach maturity by May as the temperature is rather low and ants are less active in winter. Thus it is assumed that the autumn generation is only partial, resulting in the eurychronous character of phenology.

Observations suggest that the zodariid spiders studied are mainly nocturnal (foraging in the morning and in the evening) like other Mediterranean species that have been studied. *Zodarion frenatum* Simon 1884 was found to have nocturnal activity, hunting ants mainly at dawn and dusk and searching for mates in the night (Harkness & Harkness 1992). The nocturnal activity may be due to excessive surface temperatures during the day, particularly in summer. Nocturnal activity may be an adaptation to avoid high densities of ants, which can be dangerous to hunting *Zodarion*. Current observations, however, do not support the latter hypothesis because many ants, for example *Messor*, are also active at night.

Similar to European *Zodarion* spiders, species in this study exhibited Batesian mimicry. Central European *Zodarion* spiders were found to be generalized mimics of ants (Pekár & Král 2002). They do not bear an exact resemblance to a specific model as do some corrinid spiders, for example *Myrmecium* (Hillyard 1997), but have a superficial resemblance to a group of similar ant species. Ant mimicry has been observed also in other species of the subfamily Zodariinae occurring in the Mediterranean region. Pierre (1959) suggested that *Zodariellum* (*Acanthinozodium*) *sahariense* Denis 1959 and *Zodarion bicoloripes* (Denis 1959) resemble *Messor aegyptiacus* (Emery 1878) in Algeria. In this study *Z. cyrenaicum* was found to resemble larger black (*Messor*) ants, *Z. lutipes* to resemble larger yellowish-brown (*Camponotus*) ants, and *Trygettus* to resemble tiny yellowish-brown (*Monomorium*) ants. The mimics are found in the same area as the models (Collingwood & Agosti 1996) and all these spiders closely associate with their models in order to feed on them. We failed to find a tentative model for *Z. nitidum*. It appears that males are better mimics than females, owing to the fact that females have larger abdomens. We suggest that more improved mimicry of males may be due to the different behavior of male and female *Zodarion* spiders. When running among ants, females are foraging and they retreat after capturing an ant, while males are patrolling for females and are therefore more visible to potential predators. This could select for closer mimicry in males, as it does for example in *Seothyra henscheli* Dippenaar-Schoeman 1991 (Eresidae), in which the males alone are ant mimics, while the sedentary females are not (Dippenaar-Schoeman 1991). *Messor* ants seem to be the most common ant model as many of these ants are polymorphic and can provide appropriate models for nearly all of the spiders' developmental stages.

Our results showed that *Zodarion* species are able to subdue several different ant species, as were European species of *Zodarion* (Harkness 1976; Pekár & Král 2001). Spiders ignored ants that were very small in compar-

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←

grams were made from depicted metaphases. * identifies the sex chromosome(s) at diplotenes. Note the positive heteropycnosis of the sex chromosome. Scale lines = 10 μm.

ison with the spider. It is likely that the *Zodarion* spiders studied here can feed naturally on several ant species, as does *Z. frenatum* in Greece, which hunts both *Cataglyphis* and *Messor* ants (Harkness 1976). In general, all three *Zodarion* species possess more effective venom for paralyzing Formicinae and Dolichoderinae than for Myrmicinae ants. This is consistent with results of other studies. Harkness (1976) observed in the field that *Z. frenatum* paralyzed *Cataglyphis bicolor* (Fabricius 1793) (Formicinae) ants in 15 min. Wiehle (1928) noticed that it requires about two hours for *Z. elegans* (Simon 1873) to paralyze myrmicine ants, *Messor* sp. Couvreur (1990b) found in laboratory experiments that *Z. rubidum* paralyzed several species of formicine ants in about 6 min whereas large myrmicine ants were paralyzed in about 45 min. It is believed that such effective venom against formicine ants is an important adaptation. Formicinae, in contrast to Myrmicinae, are very fast and agile. They can easily harm or even kill the spider (Schneider 1971). The attacked ant becomes aggressive and seeks the attacker but immediately after the attack, the spider retreats and waits at a distance (Pekár 2004). If the venom were less effective, the attacked ant could harm the spider or the ant could move away from the attack site and be lost to the spider. Moreover, our results suggest a certain degree of specialization in particular species. *Zodarion lutipes* may be specialized on formicine ants as it had the shortest latency to paralysis among the species studied. This species hunts and imitates *Camponotus* ants, which are very large, requiring effective venom. Also *T. sexoculatus* and *Z. cyrenaicum* both hunt the same ant species that they imitate. The former species imitates and feeds on *Monomorium* ants and the latter hunts and mimics *Messor* ants. *Zodarion cyrenaicum* was the slowest to attack of all the species studied. The explanation may lie in its specialization on myrmicine ants, which are slow moving. This is supported by recent observation when juvenile individuals of this species were seen in the vicinity of *Crematogaster nigriceps* Emery ants (Myrmicinae) (Lubin, pers. obs.). *Zodarion nitidum* was observed hunting *M. arenarius* in the field, however, it does not seem to be specialized on this species (having a long paralysis latency). Observations on ant feeding in *T. sexoculatus* support Jocqué's (1991) hypothesis that all genera of Zodariinae are either myrmecophagous or termitophagous. Females of all the species studied were better at paralyzing ants than were juveniles or males. Since it was not possible to observe how much venom was discharged at every bite, we do not know whether this difference is due to more efficient biting or to injecting more venom. The females, being larger might have more venom, however, experiments by Cushing & Santangelo (2002) showed that the size of the spider did not influence the paralysis efficiency.

Records of predators of zodariid spiders are rare (Pekár & Král 2002). Ferton (1896) described a sphecid wasp, *Psen* (*Miscophus*) *bonifaciensis* that parasitized *Zodarion elegans* and *Z. nigriceps* (Simon 1873). For the first time, an ichneumonid parasitoid attacking *Zodarion* was recorded. Since these are the only records of parasitoids, we believe that the frequency of parasitism in *Zodarion* is very low. Batesian mimicry, nocturnal activity and anachoresis, i.e. the habit of hiding in retreats (Pekár & Král 2002) may explain this low parasitism rate. *Polysphincta* wasps attack many different spider species, mainly web-building spiders (Araneidae, Dictynidae, Linyphiidae, Tetragnathidae and Theridiidae) but also hunting species living in the vegetation (Clubionidae) and occasionally epigeal species (Lycosidae) (Rollard 1984).

Courtship and copulation in *Z. lutipes* was identical to that observed in other *Zodarion* spiders (Pekár & Král 2001). Although *Zodarion* females are able to copulate repeatedly (Gerhard 1928), it seems that after a certain period, shortly before producing an egg sac, they do not copulate again. However, another copulation was recorded after the first egg sac had hatched. The copulation time of *Z. lutipes* was rather short, similar to that observed for *Z. rubidum* (Pekár & Král 2001). Females of *Z. cyrenaicum* and *Z. nitidum* copulated before they were brought to the laboratory as they refused to mate but produced egg sacs. Like in the central European species *Z. germanicum*, females guard the egg sac inside the retreat until hatching. Fecundity in all three species is higher than that found for the central European species, a likely consequence of a larger body size. Simpson (1995) found that fecundity (clutch size) is a function of the female body size in spiders and the data on *Zo-*

darion species from Israel fit his model for cursorial spiders very well.

The karyotypes of only three zodariid species, *Storena indica* Tikader & Patel 1975 (Datta & Chatterjee 1983), *Zodarion germanicum* and *Z. rubidum* (Pekár & Král 2001), have been described. Diploid chromosome numbers of males range from 22–29. Chromosome morphology of *S. indica* was not described. In the karyotype of the latter two species acrocentric chromosomes predominate. *Storena indica* and *Z. rubidum* employ a sex chromosome system X_1X_20 that is thought to be an ancestral condition in spiders (White 1973). A derived sex chromosome system X0 in *Z. germanicum*, with the acrocentric chromosome X, probably originated by tandem fusion of chromosomes X_1 and X_2. The karyotypes of the three *Zodarion* species from Israel are quite similar to each other, differing however by the length of some chromosome pairs and the type of sex chromosome system. These karyotypes are similar to karyotypes of other zodariid spiders in terms of the diploid number, sex chromosome system and morphology of chromosomes. The acrocentric sex chromosome X in the X0 system found in *Z. lutipes* and *Z. nitidum* might have originated independently from the one in *Z. germanicum*.

ACKNOWLEDGMENTS

We wish to thank O. Eitan for a translation of J. Kugler's key to the ants of Israel, P. Werner for identification of some ant species, G. Levy for additional data on fecundity and phenology and J. Šedivý for identification of the wasp. SP was funded by ARI (Advanced Research Infrastructure of EU) through the Blaustein Center for Scientific Cooperation (Blaustein Institute for Desert Research) and the Grant Agency of the Czech Republic (no. 206/01/P067). JK was supported by a grant of the Czech Ministry of Education no. 113100003. This is publication # 395 of the Mitrani Department for Desert Ecology.

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A NEW SPECIES OF *APOSTENUS* FROM CALIFORNIA, WITH NOTES ON THE GENUS (ARANEAE, LIOCRANIDAE)

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ABSTRACT. The genus *Apostenus* is newly recorded from the Nearctic region and a new species, *Apostenus californicus*, is described from California. Notes are presented on several morphological features of phylogenetic interest.

Keywords: Spiders, taxonomy, North America

The genus *Apostenus* currently comprises nine species from the western Palearctic region, including the Canary Islands, and one species each from Mongolia and Sierra Leone [although this latter species is apparently misplaced (Bosmans 1999, J. Bosselaers pers. comm.)]. Previously, three species from the Nearctic region were assigned to *Apostenus* (*A. cinctipes* Banks 1896, *A. acutus* Emerton 1909 and *A. pacificus* Gertsch 1935), but all were eventually transferred to other genera (*Dirksia* Chamberlin & Ivie 1942, *Agroeca* Westring 1861 and *Drassinella* Banks 1904, respectively) thus reinforcing the Old World distribution for the genus (Platnick & Ubick 1989). It consequently comes as quite a surprise to discover a California species that is clearly congeneric with the type species, *Apostenus fuscus* Westring 1851, in both somatic and genitalic features.

This species, which we are describing here as *A. californicus*, resembles *A. fuscus* in having the PER slightly recurved (Fig. 1), anterior tibiae with 5 and metatarsi with 3 pairs of ventral spines, tarsi with annulations and lacking true claw tufts (Figs. 3–7) and the male abdomen with modified ventral setae (Figs. 15, 16). As for genitalic features, the male of both species has a palp with a simple tapering retrolateral tibial apophysis, a narrow sickle-shaped median apophysis, and a grooved embolus (Figs. 22–24, 27–30), and the female has a median lobe on the epigynum and simple spermathecae with short copulatory ducts (Figs. 25, 26, 31, 32).

Although the California species is clearly an *Apostenus* on morphological grounds, its geographic isolation from the remaining species is puzzling. While it is certainly possible that *A. californicus* is an introduction from the Old World, this seems improbable. Unlike introduced species, which are typically found in disturbed marginal habitats and urban settings, this one has been collected from several pristine habitats of mountainous forest removed from human habitation and so appears to be a native of California. In addition, several of these mountain ranges are separated by wide stretches of low elevation habitats which appear to be impermeable barriers between the known populations and suggest a relictual presence for the species.

Assuming this to be the case, it is tempting to speculate on the biogeographical relationship between *A. californicus* and the remaining *Apostenus* species. Of some interest is the fact that a similar disjunction exists between three closely related liocranid genera. In this case, the California *Hesperocranum* Ubick & Platnick 1991 was argued to be the sister

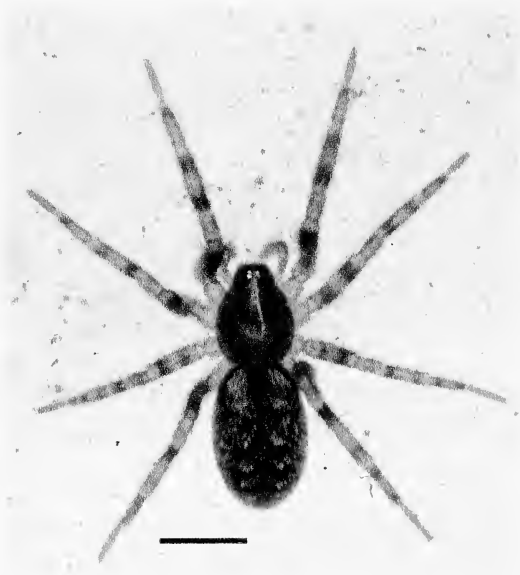


Figure 1.—*Apostenus californicus*, female, dorsal view. Scale bar = 1 mm.

group to the Palearctic *Liocranum* L. Koch 1866 and *Mesiotelus* Simon 1897 (Bosselaers & Jocqué 2002). Whether the same pattern occurs in *Apostenus* will not be known until its many poorly known species are studied.

METHODS

Observations were made using a Leica MZ12.5 dissecting microscope, Nikon SL3D compound microscope and Leica M420 dissecting microscope coupled with a JVC KY-F70B digital camera and a Syncroscopy Auto Montage system. Specimens were prepared for scanning by cleaning in a Branson 1510 Ultrasonicator, dried with a Denton DCP1 Critical Point Dryer, coated with AuPd with a Denton Vacuum Desk II Sputter Coater and examined with a Hitachi S-520 Scanning Electron Microscope.

Spiders were collected primarily by sifting oak leaf duff, both in the field and in samples brought back to the laboratory, and extracted with a Berlese funnel. Immatures removed live from the sifting were often reared to maturity. Oaks, both deciduous and perennial, were targeted as they are the most prevalent montane tree allowing leaf accumulation and subsequent decomposition in which spiders and their prey are found. Because initial *Apostenus* specimens were discovered from 1700–2100 meter elevations, collections were concentrated above the 1500 meter level. Collections were also concentrated from September through March because the rainless, summer Mediterranean climate desiccates leaf litter sufficiently that collecting is often fruitless. These factors bias the collection data presented here and may not indicate the actual availability of *Apostenus* in southern California mountains.

Description largely follows the format of Ubick & Platnick (1991). Leg and palp measurements are given as: total length (femur + tibia-patella + metatarsus + tarsus). Measurements are in mm.

Abbreviations: ALE = anterior lateral eye; ALS = anterior lateral spinneret; AME = anterior median eye; PE = posterior eyes; PER = posterior eye row; PLE = posterior lateral eye; PLS = posterior lateral spinneret; PME = posterior median eye; PMS = posterior median spinneret; RTA = retrolateral tibial apophysis.

Specimens are deposited at the California Academy of Sciences (CAS), San Diego Natural History Museum (SDM), University of California at Riverside (UCR) and the collections of T. Prentice (TRP) and D. Ubick (CDU).

TAXONOMY

Family Liocranidae
Apostenus Westring 1851
Apostenus californicus new species

Type material.—Male holotype and female allotype from moist *Quercus kelloggi* duff at intersection of Cedar Springs and Pacific Crest Trails off Morris Ranch Road, 33°40′00″N, 116°34′31″W, 2090 m, San Jacinto Mountains, Riverside County, *California*, U.S.A., 7 January 2001, R. Vetter (CAS).

Paratypes: U.S.A.: *California:* Kern County: 1 ♂, 1 juvenile, Los Padres National Forest, 100 m S of snow gate on Cuddy Valley Road toward Mount Pinos, (at mile marker 6.01), 1 km S of intersection with Cerro Mil Potrero Hwy, 34°49′51″N, 119°05′03″W, 1895 m, in moist *Quercus* shrub duff, 12 April 2003, R. Vetter (UCR); 3 juveniles, same road as above but at mile marker 8.95, 34°49′17″N, 119°05′01″W, 2105 m, in moist *Quercus kelloggi* duff, 12 April 2003, R. Vetter (UCR); Riverside County: 1 juvenile, San Jacinto Mountains: same locality as holotype, 29

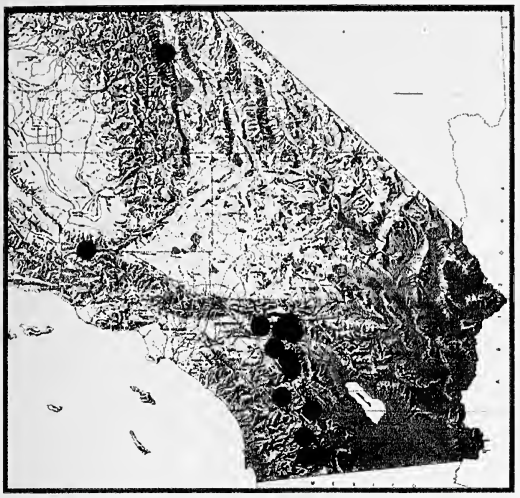
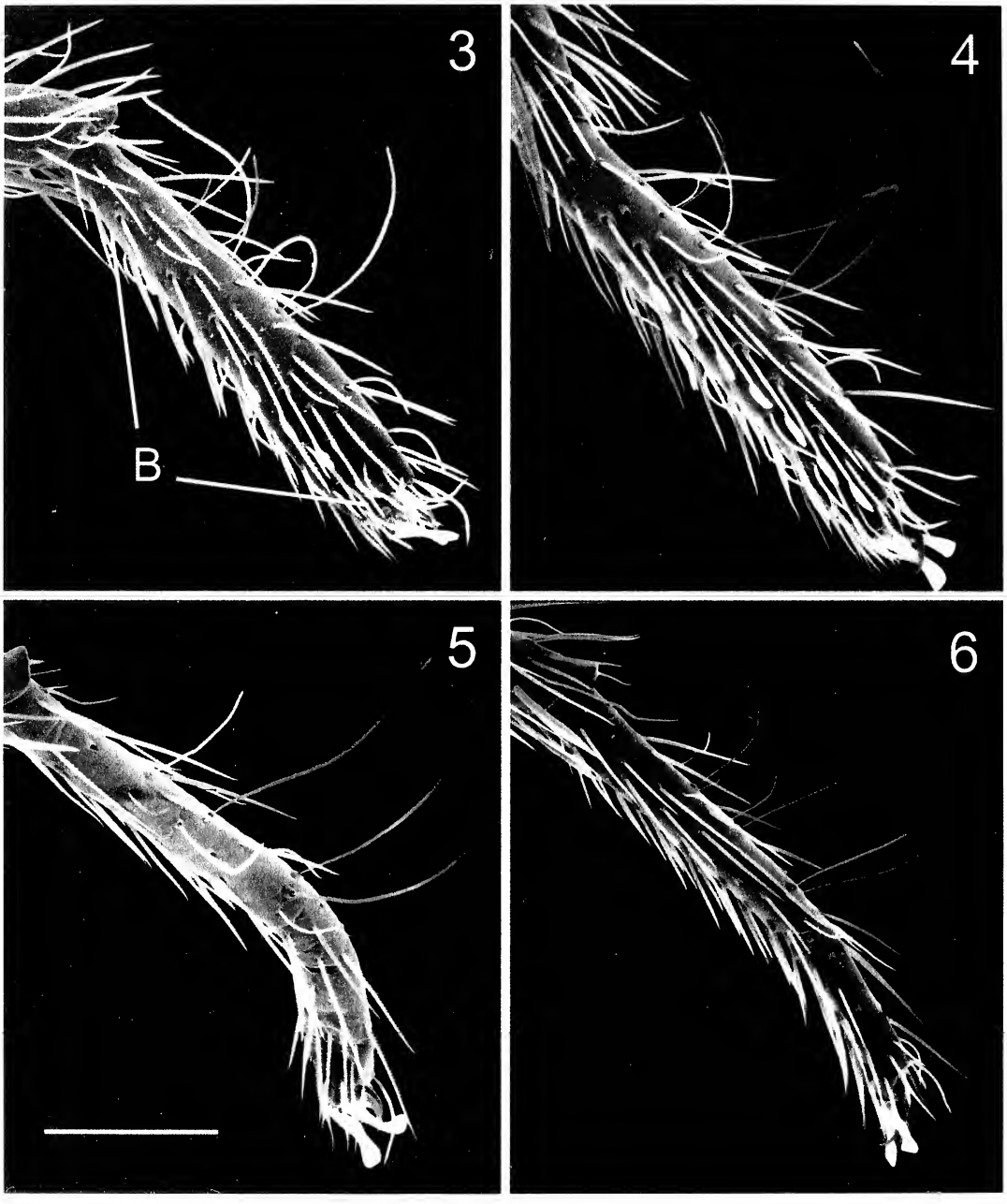


Figure 2.—Map of southern California showing the known localities of *Apostenus californicus*. The northernmost locality (Inyo County) is tentative, being based on juvenile specimens.

March 2001; 4 juveniles (3 ♀ reared to maturity), 28 April 2001; 1 juvenile, along Cedar Springs Trail (Trail 4E17), 1950 m, in dry *Quercus wislizenii* duff, 7 January 2001; 6 ♂, 6 ♀, 9 juveniles (1 ♀ reared to maturity), on Cedar Springs Trail off Morris Ranch Rd., 33°39′42″N, 116°34′41″W, 1790 m, in moist *Quercus chrysolepis* duff, 30 September 2001; 4 females, 4 juveniles, near Cedar Springs trailhead, 33°39′26″N, 116°35′01″W, 1720 m, in dry *Quercus chrysolepis* oak duff near streambed, 7 January 2001; 1 juvenile, in moist *Quercus chrysolepis* oak duff under snow, 18 March 2001; all above collected by R. Vetter (6 ♂ and 4 ♀ at CAS, remainder at UCR); 2 ♂, 2 ♀, 1 juvenile, James Reserve, Lake Fulmor, 33°48′31″N, 116°46′36″W, 1640 m, in dry *Quercus kelloggi* oak-pine duff next to wet stream, 8 October 2001, R. Vetter and T. Prentice (UCR); 1 ♀, 4.2 km N Lake Fulmor on Hwy 243, trailhead of trail 2E35, 33°49′39″N, 116°47′44″W, 1575 m, in extremely dry *Quercus* leaf duff, 26 September 2003, R. Vetter (UCR); 1 ♀, 1 juvenile, Spillway Canyon, S of Lake Hemet, 33°39′07″N, 116°41′32″W, 1365 m, probably from oak litter, 29 May 2001, T. Prentice & D. Popko (UCR); San Bernandino County: San Bernardino Mountains: 1 ♀, 4.8 km W Angelus Oaks general store on Hwy 38, 34°10′N, 116°52′W, 1820 m, in *Quercus kelloggi* duff, 6 June 2003, R. Vetter (UCR); 1 ♀, Forest Falls, Momyer-Alger Trail, 34°05′05″N, 116°55′07″W, 1660 m, 1 April 2001, T.R. Prentice (TRP); 6 juveniles (1 ♂, 2 ♀ reared to maturity), in oak duff, 28 May 2001, T. Prentice (UCR); 1 juvenile (♀ reared to maturity), 17 April 2002, T. Prentice (TRP); 1 ♀, 2 juveniles, Forest Falls, near Vivian Creek trailhead (Trail 1E08), 34°04′58″N, 116°53′35″W, 1850 m, in dry scrub oak duff, 25 March 2001, R. Vetter (UCR); 2 ♀, 3 juveniles, 1 April 2001, T. Prentice (TRP); 1 juvenile, Forsee Creek and Hwy 38, 0.4 mi E of Camp Cedar Falls turnoff, 34°09′29″N, 116°55′54″W, 1850 m, in *Quercus* sp. duff, 15 June 2003, R. Vetter (UCR); 1 ♀, 1 km W Jenks Lake Loop Road East turnoff, 34°10′14″N, 116°50′29″W, 2093 m, in scrub oak duff, 6 May 2001, R. Vetter (UCR); 1 penultimate male, Ponderosa Pines trail (1E19) near W entrance to Jenks Lake Loop Road on Hwy 38, 34°09′56″N, 116°54′46″W, 1950 m, in *Quercus* sp. duff, 15 June 2003, R. Vetter (UCR); 3 ♀, 6 juveniles, Mill Creek Canyon, 1.3 km E of Hwy 38 on Valley of the Falls Dr., 34°05′42″N, 116°56′44″W, 1450 m, 2 March 2002, R. Vetter (UCR); 1 juvenile, near Seven Oaks, 1.6 km N of Hwy 38 on Glass Rd, 34°10′29″N, 116°54′00″W, 1820 m, in mixed *Quercus kelloggi* and pine duff, 6 May 2001, R. Vetter (UCR); 1 ♀, 1 juvenile, in *Quercus kelloggi* and *Q. chrysolepis* duff, 6 June 2003, R. Vetter (UCR); 1 ♀, 3 juveniles, Skinner Ridge between Skinner Creek and Mountain Home Creek, 34°06′48″N, 116°58′53″W, 1500 m, in oak duff, 29 November 1983–26 January 1984, M. Narog (UCR); 1 ♂, 23 January 1986, M. Narog (UCR); San Diego County: 1 ♂, 5 ♀, 1 penultimate ♂, 3 juveniles, Cleveland National Forest, Julian, 4839 Pine Ridge Ave., 33°02′34″N, 116°37′49″W, 1300 m, in mixed *Quercus kelloggi* and *Quercus* sp. leaf duff, 31 March 2002, R. Vetter (UCR); 2 penultimate ♂, Cleveland National Forest, ca. 1.6 km N Cibbets Flat, 32°46′38″N, 116°26′56″W, 1250 m, 12 July 2003, J. Berrian (SDM); 1 ♂, 1 ♀, Descanso Junction, 32°50′N, 116°36′W, 1040 m, ex willow duff, 31 March 1961, E. Lindquist (CDU); 4 juveniles, Laguna Mountain across from fire station, 1/8 mi N Camp Ole Station, 32°53′N, 116°25′W, 1755 m, in duff of black oak, *Quercus kelloggi*, 20 February 2003, L. Merrill and R. Vetter (UCR); 2 ♀, Palomar Mountain State Park, Doane Pond trail, 20 m from parking lot, 33°20′29″N, 116°54′05″W, 1415 m, in mixed *Quercus* oak



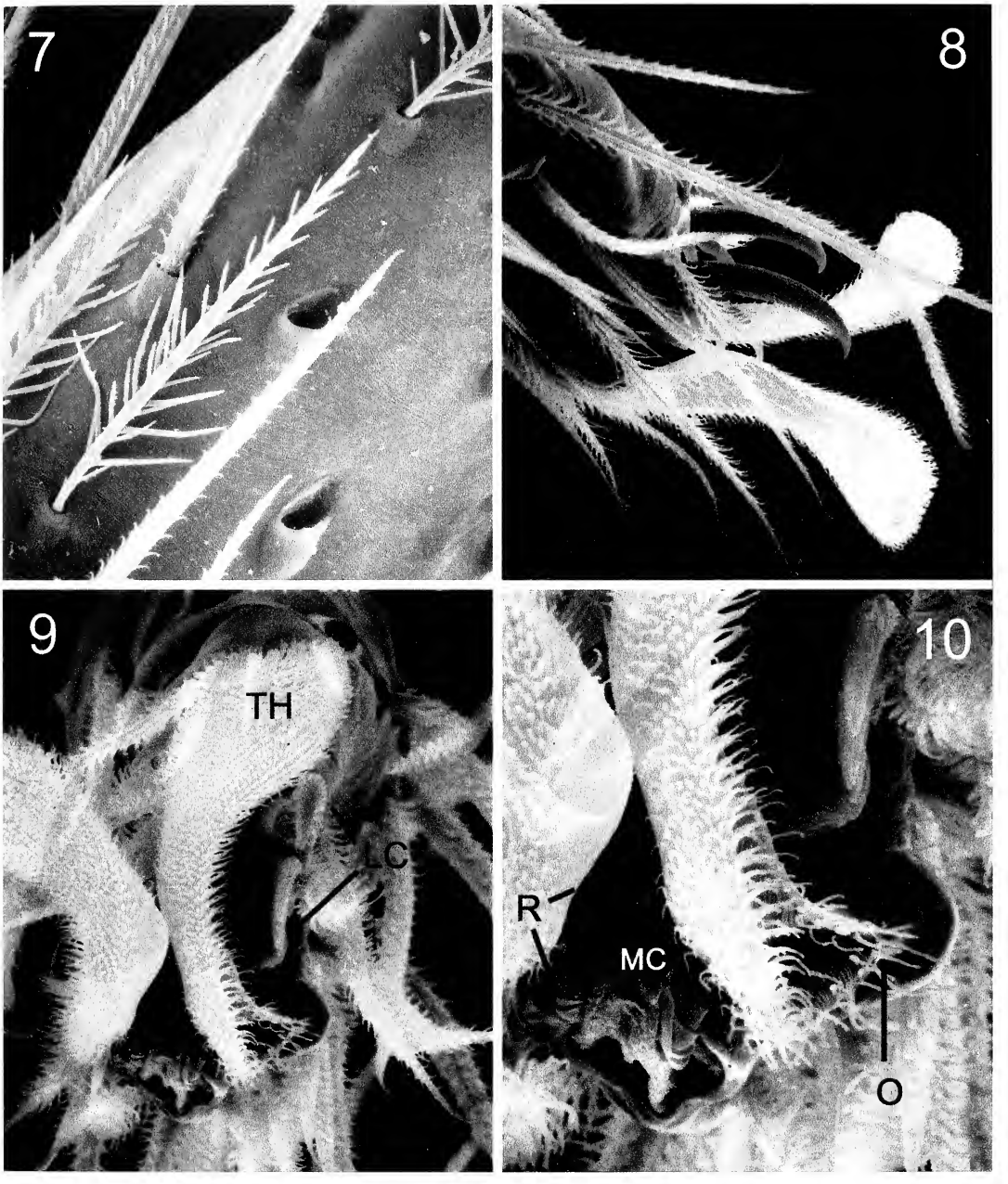
Figures 3–6.—*Apostenus californicus*, lateral views of tarsi: 3, 4. Tarsus I showing leg bristles (B); 5, 6. Tarsus IV; 3, 5. Male; 4, 6. Female. Scale bar = 150 um (3–5), 200 um (6).

duff on creek bank next to road, 20 January 2003, R. Vetter (UCR); 1 ♀, 0.3 mi W of Ranchita on Hwy S22, 33°12′37″N, 116°32′30″W, 1193 m, in oak leaf duff, 16 March 2003, R. Vetter (UCR).

Non-paratypes (identification tentative): U.S.A.: *California:* 2 juveniles, Inyo County: Independence: Oak Creek Campground, just beyond Mt. Whitney Fish Hatchery, 36°50′31″N, 118°15′37″W, 1455 m, in black oak duff, 7 May 2003, E.F. Drake (UCR).

Etymology.—The species name refers to its known distribution.

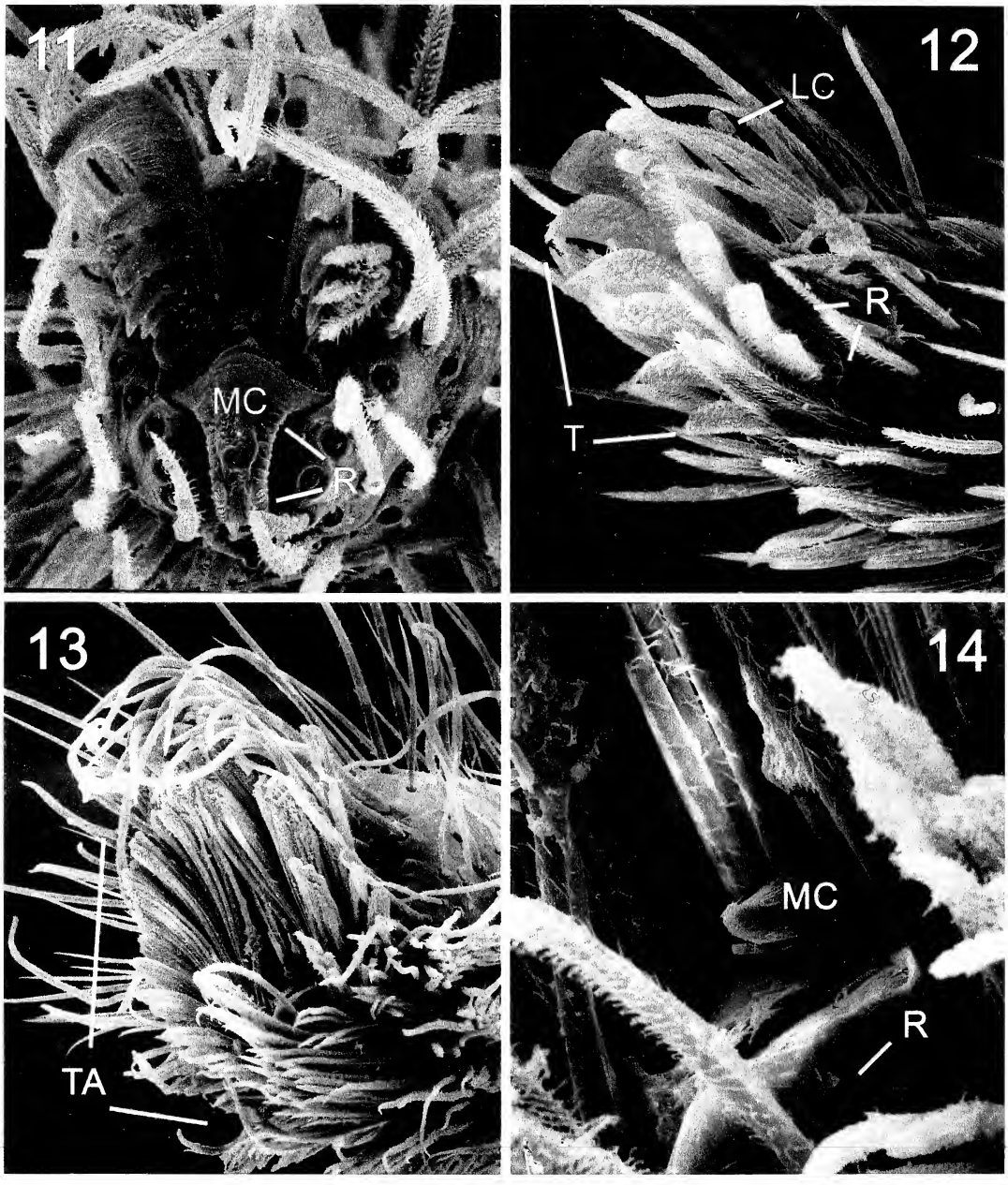
Diagnosis.—This is the only *Apostenus* known from the Nearctic region. The male is similar to *A. annulipedes* Wunderlich from



Figures 7–10.—*Apostenus californicus*, male leg parts: 7. Tibia IV showing plumose hair; 8–10. Apices of tarsus I; 8. Lateral view; 9. Apical view showing enlarged tenent hairs (TH) and lateral claw (LC); 10. Close-up of apical view showing median claw scar (MC) with lateral ridges (R) and origin of tenent hair laterad of lateral claw (O).

which it differs in having the median apophysis longer and originating more basad on the bulb. The female is close to *A. grancanariensis* Wunderlich (male unknown) but has the spermathecae more widely separated. (compare Figs. 22–26 with figs. 750e–h and 751–751a in Wunderlich 1992).

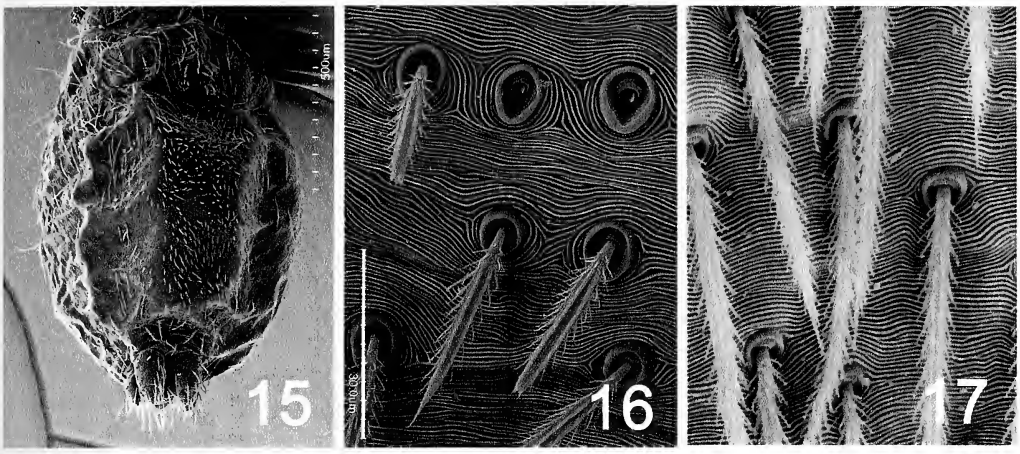
Description.—*Male (holotype, range of other males in parentheses; n = 8):* Total length 2.42 (2.24–2.95). Carapace length 1.10 (0.98–1.15), width 0.88 (0.79–0.94), height 0.34. Clypeus 0.08 (at AME), 0.05 (at ALE). Fovea length 0.18. Abdomen length 1.32, width 0.74. Eye sizes and interdistances:



Figures 11–14.—Apices of tarsus I of various spiders: 11. *Liocranum* sp., apical view showing median claw scar (MC) with lateral ridges (R) and the absence of a tuft or tenent hairs; 12. *Drassinella* sp., lateral view showing lateral claw (LC) and tuft (T) arising from lateral ridges (R) of median claw scar; 13–14. *Titiotus* sp.; 13. Lateral view showing claw tuft analog (TA); 14. Close-up showing reduced median claw (MC) with lateral ridges (R).

AME 0.04, ALE 0.08, PME 0.06, PLE 0.06, AME-AME 0.03, AME-ALE 0.02, PME-PME 0.06, PME-PLE 0.04, ALE-PLE 0.04, AER 0.25, PER 0.30. Palpus and leg lengths: Palpus: 1.10 (0.38 + 0.34 + 0 + 0.38); Leg I: 3.38 (0.90 + 1.22 + 0.64 + 0.62); Leg II: 2.96 (0.84 + 1.02 + 0.58 + 0.52); Leg III: 2.84 (0.76 + 0.94 + 0.64 + 0.50); Leg IV: 4.06 (1.06 + 1.34 + 0.98 + 0.68). Leg formula 4123.

Color: Carapace brown, black in eye region and along margin, light brown at fovea. Ab-



Figures 15–17.—*Apostenus californicus*, abdomen: 15, 16. Male; 15. Ventral view showing distribution of modified setae along midline; 16. Close-up of modified setae; 17. Female, comparable part of abdomen showing unmodified setae. Scale bar = 500 um (15), 30 um (16, 17).

domen dorsum dark brown to black with two short longitudinal pale marks anteriorly, followed by two pairs of transverse marks, and 2–3 transverse bands posteriorly; venter light brown with dark median maculation. Legs light brown with dark annulations, anterior femora and tibia dark brown, coxae light brown. Sternum brown.

Vestiture: Carapace largely glabrous, eye region and clypeus with strong setae and recumbent white scales in longitudinal band. Sternum with setae mostly at margins and at posterior projection. Abdomen dorsum densely setose, anteriorly with recumbent white setae, venter with modified short setae (Figs. 15, 16); appendages densely clothed with long setae, spines, plumose hairs and trichobothria.

Carapace piriform in dorsal view, somewhat flattened, highest at fovea. AME smallest, about half the diameter of ALE, PE subequal slightly smaller than ALE, AER straight, PER slightly recurved in dorsal view. Chelicerae not geniculate, lacking boss, anterior face with several setae, no spines, retromargin with 2 teeth, promargin with 3 teeth. Sternum rounded, anteriorly truncate, with posterior extension between coxae IV, with marginal setae, especially at posterior extension. Precoxal triangles absent. Labium rounded, wider than long, one half length of endites; endites quadrate, with serrula on anterior margin.

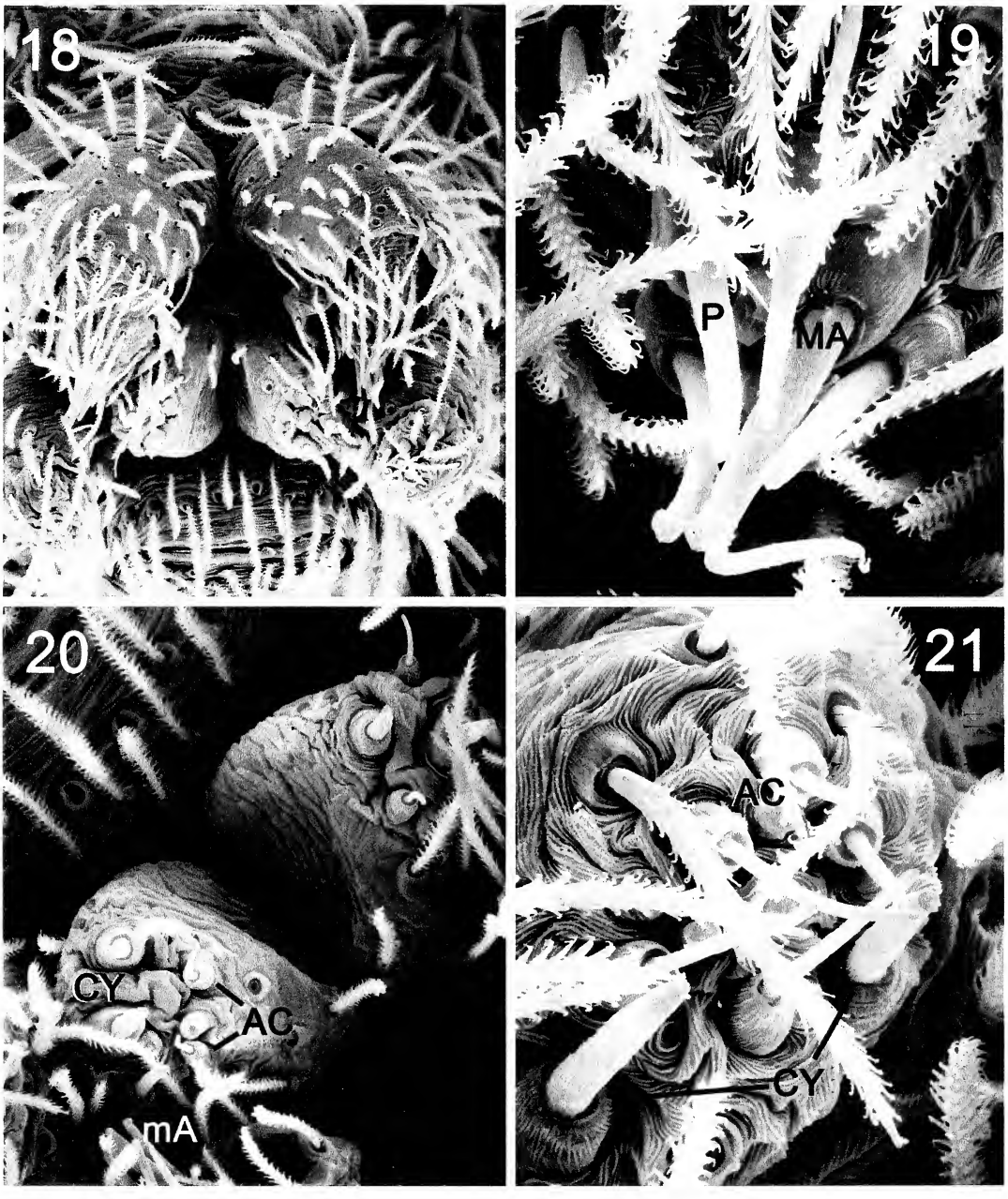
Abdomen: lacking dorsal scute; epigastric furrow lacking epiandrous spigots. Spinnerets with colulus represented by two setae; ALS conical, 2-segmented, contiguous, twice the width of the PLS; ALS with 3 spigots (piriform) and 3 nubbins; PMS with 3 spigots (aciniform) and 2 nubbins; PLS with 3 spigots (aciniform) and 3 nubbins.

Tarsi, metatarsi, and tibiae with dorsal trichobothria in two rows. Tarsi subsegmented; anterior with lateroventral rows of spatulate bristles (Fig. 3); posterior longer than anterior, bent in apical third (Fig. 5); with two pectinate lateral claws and two broad tenent hairs originating laterad of claws (Figs. 8–10). Leg spines: I: metatarsus v2–2–2, tibia v2-2-2-2-2, femur d1–1–0, p0–0–1, v0-0-0-8 (bristles); II: metatarsus v2–2–2, tibia v2-2-2-2, femur d1–1–0, v0-0-0-8 (bristles); III: tibia d2–1, v1–1–0; IV: metatarsus d2–2–0, v2–2–0, tibia d1–2–2, v2–2–0.

Palpus: Cymbium with dorsoapical scopula, lacking trichobothria. Bulb with median apophysis sickle-shaped, conductor absent, embolus broad with apical groove and angular base which forms a lock with the subtegulum. RTA short, curved, thorn-like prong. Femur lacking ventral process. (Figs. 22–24, 27–30)

Variation: Penultimate males lack the modified setae on the venter of the abdomen and the recumbent scales on the carapace and abdomen.

Female (allotype, range of other females in parentheses; n = 8): Total length 3.14 (2.30–3.60). Carapace length 1.14 (1.05–1.32), width 0.94 (0.85–1.05), height 0.47. Clypeus



Figures 18–21.—*Apostenus californicus*, female spinnerets: 18. entire spinning field; 19. ALS, showing major ampulate (MA) and piriform (P) spigots; 20. PMS, showing minor ampulate (mA), cylindrical (CY), and aciniform (AC) spigots; 21. PLS, showing cylindrical (CY) and aciniform (AC) spigots.

0.08 (at AME), 0.04 (at ALE). Fovea length 0.14. Abdomen length 1.80, width 1.14. Eye sizes and interdistances: AME 0.04, ALE 0.08, PME 0.07, PLE 0.07, AME-AME 0.03, AME-ALE 0.02, PME-PME 0.05, PME-PLE 0.03, ALE-PLE 0.05, AER 0.34, PER 0.26. Palpus and leg lengths: Palpus: 1.12 (0.40 + 0.38 + 0 + 0.34); Leg I: 3.28 (0.98 + 1.20 + 0.64 + 0.46); Leg II: 3.02 (0.90 + 1.10 + 0.60 + 0.42); Leg III: 2.86 (0.78 + 0.98 + 0.60 + 0.50); Leg IV: 3.98 (1.06 + 1.36 + 0.94 + 0.62). Leg formula 4123.

Color as in male. Vestiture as in male except that abdominal venter has long slender

setae and the carapace and abdomen lack the conspicuous recumbent scales. Form essentially as male except that tarsi are shorter and tarsi IV straighter than in male.

Epigynum with rounded lateral lobes and triangular median lobe; copulatory openings in median grooves. Vulva with 2 rounded spermathecae, short copulatory ducts, and curved fertilization ducts. Spinnerets as in male; PMS conical, not compressed; ALS with 6 long spigots (4 piriforms and 2 larger major ampulates); PMS with 2 large cylindrical spigots, 1 smaller minor ampulate, and 3 small aciniforms; PLS with 2 cylindrical and 5–6 aciniform spigots (Figs. 18–21).

Sexual dimorphism: Adult males have a vestiture of short setae on the abdominal venter and recumbent white scales on the carapace and abdominal dorsum. Males have tarsi longer, and posterior tarsi more strongly bent, than females.

Biology.—This species is widespread in the mountains of southern California and has been collected from several contiguous localities each in San Diego County and the San Jacinto and San Bernardino Mountains. It is also known from two isolated localities to the west in Kern County, and a tentative record, based on juveniles, to the north in Inyo County. The spider occurs in leaf litter (which varies from moist to slightly dry) of various oak species (with two records from oak and pine duff and one from willow) at elevations from 1040–2100 m. Males have been taken from September–April, females from September–June. In the lab, juvenile *Apostenus* were successfully reared to maturity on a diet of Collembola, Psocoptera, and Lepidoptera larvae.

Distribution.—Known only from southern California (Fig. 2).

DISCUSSION

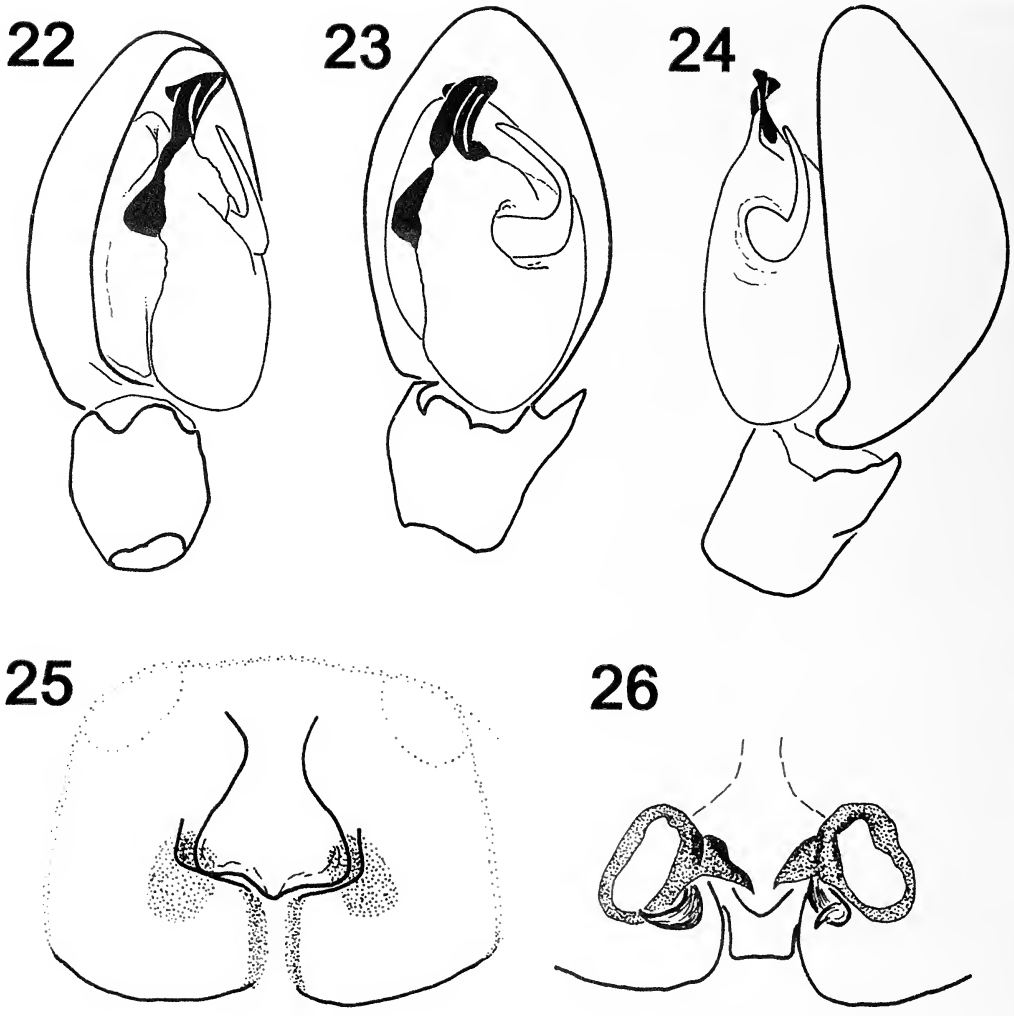
Our examination of *A. californicus* has turned up some observations that have not been adequately, if at all, described in the literature. To date, the most complete description of *Apostenus* is in the recent analysis of the clubionoid genera by Bosselaers & Jocqué (2002), to which we can add the following:

Dimorphic abdominal setae.—The presence of short setae ventrally on the male abdomen (Figs. 15, 16) was not scored by Bosselaers & Jocqué (2002), but occurs in *A. californicus* and *A. fuscus* and appears to be an autapomorphy for *Apostenus*. Although Wunderlich (1999) refers to the presence of modified setae in some species of *Agroeca* Westring 1861, of the species we examined, the males have normal setae (*A. minuta* Banks 1895, *A. pratensis* Emerton 1890, and *A. trivittata* (Keyserling 1887)), slightly shorter setae (*A. ornata* Banks 1892) or short ones interspersed with normal setae (*A. brunnea* (Blackwall 1833), J. Bosselaers pers. comm.).

Claw tufts.—The tip of the tarsus bears two spatulate tenent hairs (Figs. 8–10) which also appear to be an autapomorphy for the genus. Although this was interpreted as a claw tuft by Bosselaers & Jocqué (2002: Character 63), it is clearly not homologous to a true tuft, which is generally understood to arise from the transformed median claw (Forster 1970). In *Apostenus californicus*, the modified hairs originate laterad of the paired claws and the region of the median claw is represented by a vestige consisting of a central protuberance and a series of lateral ridges (Figs. 9, 10). In a true claw tuft, the modified setae originate from the lateral ridge portion of the median claw vestige, as for example in *Drassinella* (Fig. 12). Such tufts are of a different origin, as are the tufts in 3-clawed spiders. Forster (1970) recorded various forms of claw tuft analogs in several 3-clawed desid genera from New Zealand, and similar analog tufts are also found in the 3-clawed *Titiotus* Simon 1897 and related tengellids from the Nearctic region (Figs. 13, 14). Finally, claws lacking tufts of any sort are found in several liocranid genera, for example, in *Liocranum* (Fig. 11). Detailed observations of these structures will be necessary to determine homology.

Bent posterior tarsi.—All tarsi are subsegmented in both sexes of *Apostenus*, but tarsi III & IV are much more markedly bent in the male (Figs. 3–6). Subsegmented and bent posterior tarsi occur in several Holarctic liocranid genera (*Agroeca*, *Agraecina* Simon 1932, *Cybaeodes* Simon 1878, *Neoanagraphis* Gertsch & Mulaik 1936, and *Scotina* Menge 1873). This character was first noted by Wunderlich (1999) and interpreted as a synapomorphy by Bosselaers & Jocqué (2002: Character 9) for this group of genera. Interestingly, in *Apostenus* the subsegmented tarsi occur in both sexes, but only in males of *Agroeca* and *Neoanagraphis*.

Tegulum/subtegulum lock.—The locking



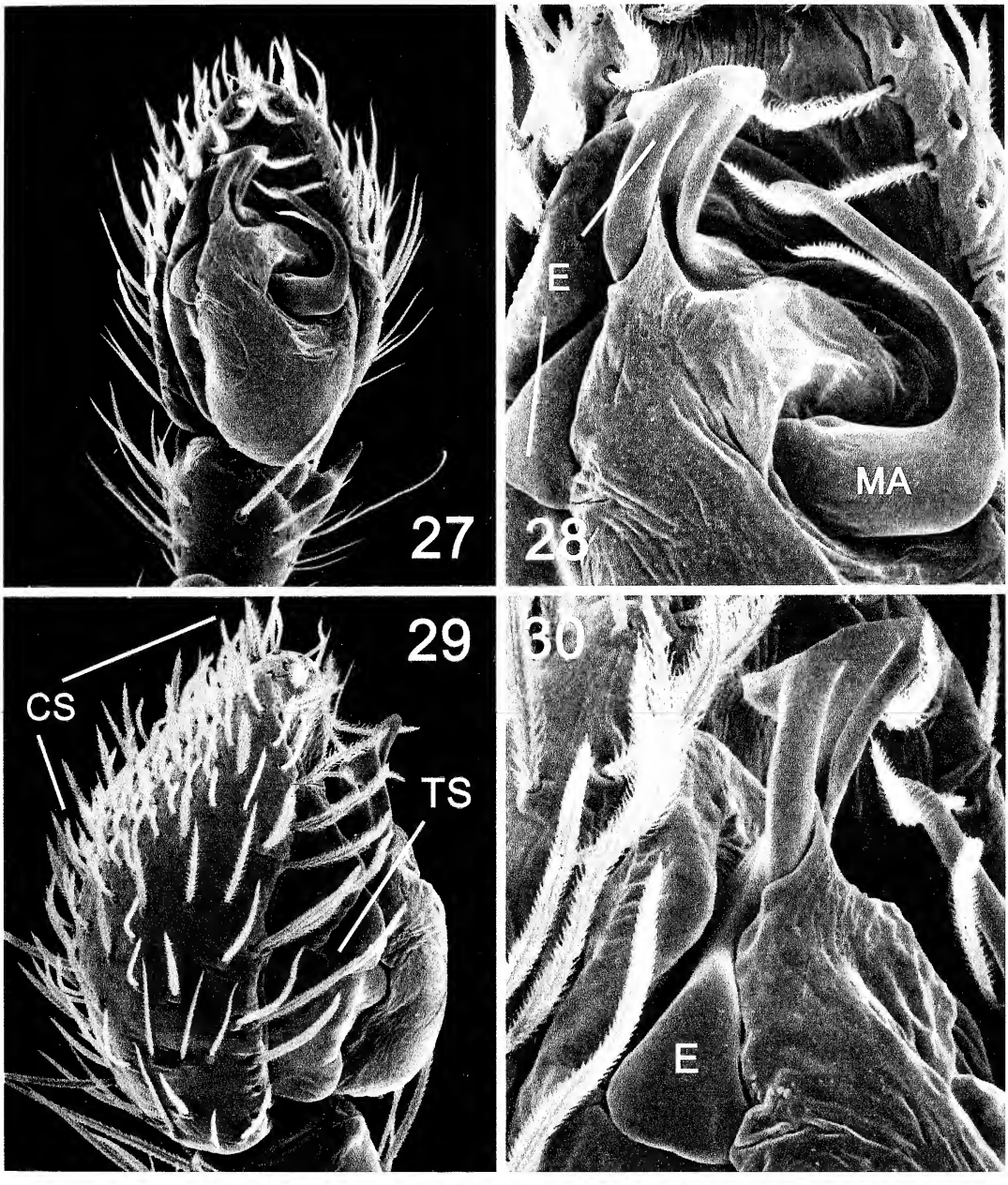
Figures 22–26.—*Apostenus californicus*, genitalia: 22–24. Male left palpus with embolus in black; 22. Prolateral-ventral view; 23. Ventral view; 24. Retrolateral view; 25, 26. Female epigynum; 25. Ventral view; 26. Dorsal view.

mechanism of the tegulum to subtegulum was first observed by Griswold (1993) in the Lycosoidea and its basal sister groups. A similar locking structure occurs in *Apostenus* (Figs. 22, 29), which has a distinct subtegular lobe, but may differ in having the tegular lobe represented by the embolar base. This locking mechanism was also recorded in *Agroeca*, *Scotina*, and *Phrurotimpus* Chamberlin & Ivie 1935 (Bosselaers & Jocqué 2002: Characters 130, 131).

Cymbial scopula.—A scopula on the dorsoapical part of the cymbium was not noted by Bosselaers & Jocqué (2002), but occurs in *Apostenus californicus* (Fig. 29), at least in some *Agroeca* (observed in *A. pratensis*), and is also found in a number of lycosoids and their kin (Griswold 1993).

Epigynum with scape.—Bosselaers & Jocqué (2002, Character 148) interpreted the middle piece of the epigynum of *Apostenus* as a scape. But unlike a scape, it is broadly attached to the rest of the epigynum (Figs. 25, 31, 32) and more closely resembles the median lobe of amaurobiids, lycosoids, and some other spiders.

Embolus insertion.—Although the embolus of *A. californicus* is apical in position, its insertion as seen in prolateral views is clearly at the middle of the bulb (Figs. 22, 29, 30)



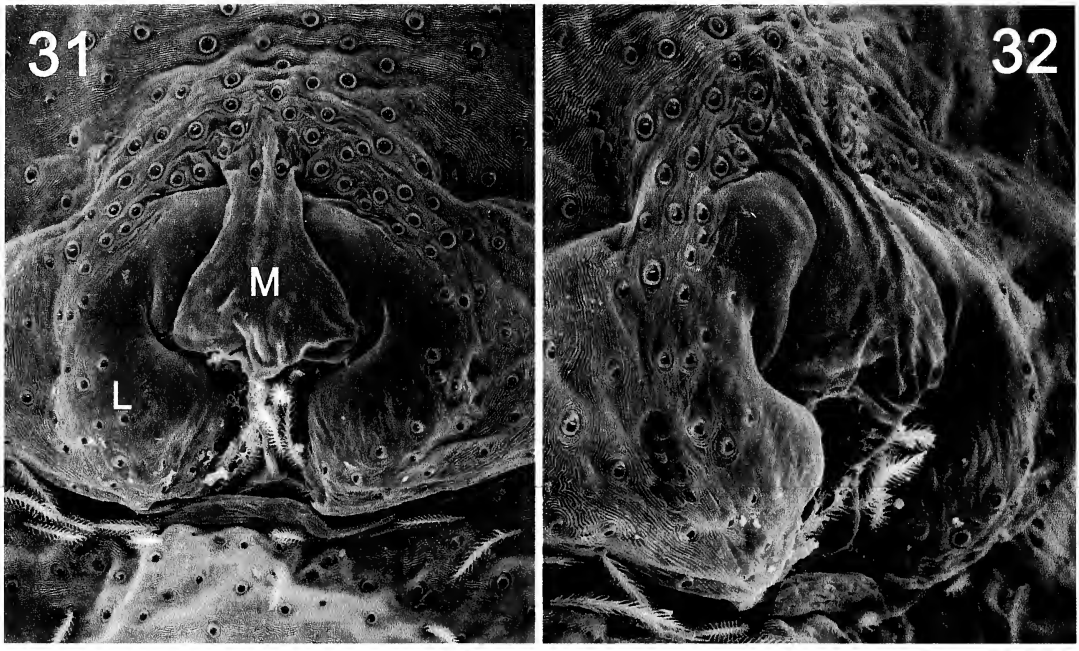
Figures 27–30.—*Apostenus californicus*, male left palpus: 27, 28. Ventral view with close-up showing embolus (E) and median apophysis (MA); 29, 30. Prolateral view showing cymbial scopula (CS) and tegular-subtegular locking mechanism (TS) and a close-up showing base of embolus (E).

and not apical as recorded by Bosselaers & Jocqué (2002: Character 140)

Abdominal scute.—Bosselaers & Jocqué (2002) indicate the presence of a male abdominal scute in *Apostenus* (Character 102); but this was not observed in *A. californicus*.

Plumose hairs.—Bosselaers & Jocqué (2002) state that *Apostenus* lacks plumose hairs (Character 57); in *A. californicus* they are present on the legs (Fig. 7).

Leg bristles.—These bristles have been interpreted as diminutive spines (Ubick & Platnick 1991) and occur in a wide number of clubionoids. Although they were not recorded for *Apostenus* by Bosselaers & Jocqué (2002, Characters 4 & 5), they are present in *Apos-*



Figures 31–32.—*Apostenus californicus*, female epigynum, setae removed: 31. Ventral view showing lateral (L) and median (M) lobes; 32. Ventrolateral view.

tenus californicus (Figs. 3, 4), and also occur, at least on anterior tarsi, in other species of *Apostenus* and in *Agroeca* and *Liocranoeca*.

The family placement of *Apostenus* is presently in a state of flux. Although traditionally associated with the Liocranidae, the most recent analysis of the clubionoid genera (Bosselaers & Jocqué 2002), argues that the genus belongs neither to the Liocranidae, *sensu stricto*, nor to the Phrurolithinae (which they transferred to the Corinnidae) but to an intermediate clade which was not assigned to family. As mentioned above, the genus appears to cluster with the several genera having subsegmented tarsi. These genera also lack claw tufts and precoxal triangles and show some affinities to the lycosoid complex, suggested by the bulbal locking mechanism and cymbial scopula, which may be worth exploring further.

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THE EFFECT OF PERCEIVED PREDATION RISK ON MALE COURTSHIP AND COPULATORY BEHAVIOR IN THE WOLF SPIDER *PARDOSA MILVINA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. The wolf spider, *Pardosa milvina* (Hentz 1844), shows effective antipredator responses in the presence of chemotactile cues (silk and excreta) from a larger wolf spider, *Hogna helluo* (Walckenaer 1837). We examined the influence of these substratum-borne cues on male *P. milvina* courtship and copulatory behavior. Forty-one pairs of adult virgin male and female *P. milvina* were placed on substrates with or without silk and excreta from an adult female *H. helluo*. Using behavioral observation software (Noldus Observer® 4.1), we recorded time until courtship, courtship duration, and intensity (leg raise and body shake rates). We also measured the total number of matings, the duration of each mating, and the number and rate of successful and failed palpal insertions. While we found no difference between treatments in mating success, courtship intensity or duration, there were significant increases in time until courtship and significant decreases in palpal insertion rates under predation risk. Males under predation risk also had significantly more failed palpal insertions than males not under risk. Results suggest that predation risk has a relatively minor impact on courtship displays and mating success, but could potentially impact mate searching, sperm transfer efficiency, or copulatory courtship.

Keywords: *Hogna helluo*, kairomone, mate choice, mating, chemical cue

Most wolf spider species engage in conspicuous courtship displays that include leg-waving, stridulating, drumming, tapping or other attention-drawing signals (Kaston 1936; Rovner 1967a, 1968, 1975; Stratton & Uetz 1986; Hebets & Uetz 2000). These visual and vibratory displays often significantly increase mating success of the males (Hebets & Uetz 2000; McClintock & Uetz 1996; Parri et al. 1997, 2002; Rypstra et al. 2003), but may also attract the attention of predators (Kotiaho et al. 1998). Males may mitigate the costs of courtship displays by reducing courtship intensity or duration when predation risk is elevated, however this may compromise species recognition or assessment of male quality by the female and contribute to lower mating success (Kotiaho et al. 1996, 1998).

Male courtship displays may not be the only component of lycosid mating behavior to be compromised by predation risk. Many species engage in prolonged copulation (Stratton et al. 1996) that could lead to reduced vigilance or physical impairment of the ability of either the male or female to quickly escape from a predator. During copulation, wolf spiders may perform a variety of conspicuous behaviors including rapid bouncing or vibrating of the abdomen by the male (Kaston 1936) and abdominal rotations by the female to facilitate pedipalp-epigynal coupling (Stratton et al. 1996). In addition to these movements, the male often scrapes, rubs or taps at the epigynum with his palps and engages in various repositioning movements as the male moves from one side of the female to the other (Kaston 1936; Rovner 1967b; Stratton et al. 1996). If these overt copulatory behaviors also attract attention from predators, pairs may benefit by minimizing their frequency or abbreviating copulation duration when predation risk is high.

Several recent studies have shown that the wolf spider, *Pardosa milvina* (Hentz 1844), is capable of detecting and responding to silk and excreta deposited by a larger syntopic

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wolf spider, *Hogna helluo* (Walckenaer 1837) (Persons & Rypstra 2001; Barnes et al. 2002; Persons et al. 2002). Upon encountering these cues from *H. helluo*, *P. milvina* typically greatly reduce their activity level and show increased vertical movement and substratum avoidance (Persons & Rypstra 2001; Persons et al. 2001, 2002). These behavioral shifts have a probable defensive function since *P. milvina* that reduce activity when encountering *H. helluo* silk and excreta survive significantly longer when confronted with live *H. helluo* than individuals that do not have access to these cues (Persons et al. 2001, 2002; Barnes et al. 2002). If *P. milvina* shows adaptive reductions in activity when encountering cues from *H. helluo*, presumably, the presence of these cues may also alter *P. milvina* courtship and mating behavior. Here we tested the influence of predation risk on *P. milvina* courtship and mating behavior by using *H. helluo* silk and excreta as a proxy for a live predator.

METHODS

Collection and Maintenance.—Between August and October 2002, we collected 82 intact *P. milvina* from corn, soybean and alfalfa fields near Susquehanna University, Selinsgrove, Snyder County, PA. To ensure that all spiders used in our mating experiment were virgins, we collected only antepenultimate and penultimate male and females and reared them to maturity in the laboratory. We also collected adult female *H. helluo* to be used for the deposition of silk and excreta as the source of predator cues. Both species of spider received food and water weekly. Diets consisted of 3–5 adult and subadult house crickets (*Acheta domesticus*) for *H. helluo* and 5–7 one-week-old cricket nymphs (*A. domesticus*) and adult fruit flies (*Drosophila melanogaster*) for *P. milvina*. Housing for *H. helluo* consisted of white round plastic containers (8 cm in height × 11 cm in diameter) with two to three cm of moistened peat moss as a substratum. *Pardosa milvina* were kept in clear round plastic containers of smaller size (5 cm in height × 8 cm in diameter) with one to two cm of the moist peat moss substrate. Spiders were maintained at room temperature (23–25 °C) with a 14:10 L:D photoperiod.

Stimulus Preparation.—We prepared 41 courtship and mating arenas that either did (n = 20) or did not (n = 21) have silk and excreta from a single adult *H. helluo*. Each arena consisted of a transparent plastic container (Rubbermaid Tortilla Keeper®, 9 cm h × 20 cm diam.). Forty-eight hours prior to testing, a 20 cm diam. circular sheet of white filter paper was placed on the bottom of each arena along with an inverted 15 dram vial lid containing several drops of water. The lid served as a means of providing humidity and a direct source of water to stimulus spiders during cue deposition. A single adult virgin female *P. milvina* was then introduced into each arena and allowed to move freely for a 24 h period. For the no-predator cues treatment, the female was then removed for an additional 24 h prior to being paired with a male. For the predator cues treatment, the female *P. milvina* was also removed for an additional 24 h; but immediately after removal, we introduced a single adult female *H. helluo* into the container where she was allowed to lay down silk and excreta on the filter paper for 24 h. The *H. helluo* was then removed from the arena immediately prior to testing. A different *H. helluo* was used to deposit predatory cues for each male-female *P. milvina* pair in the predator cue treatment. During stimulus preparation, we satiated both the adult female *P. milvina* and the female *H. helluo* by providing constant access to appropriately sized *A. domesticus* 24 h before their introduction into the arena to deposit silk and excreta. We also satiated adult male and female *P. milvina* pairs using the same method before the beginning of the trial. This served to reduce variation in body condition among paired spiders, a possible confounding variable in the female's mate choice decision or male display rates. All *P. milvina* tested had been between four and fourteen days post-final molt and all pairs were alternately assigned to either treatment to control for possible temporal effects on mating or copulatory behaviors between treatments.

Testing Protocol.—Following the removal of *H. helluo*, females were then reintroduced into their respective containers and allowed to acclimate for fifteen minutes, after which the males were introduced into the center of the arena under a clear plastic vial (15 dram). Males were allowed a two minute acclimation period under the vial after which time they were released and allowed to freely interact

Table 1.—Male *Pardosa milvina* behavior with (Predator cues) and without (No predator cues) the presence of silk and excreta from an adult female *Hogna helluo*. Each behavior was analyzed using a two-sample t-test. Mean ± SE for each behavior is reported. * indicates significant difference after a table-wide adjustment to the alpha level (sequential bonferroni).

Behavior	*n*	Predator Cues	No Predator Cues	*T*-value	*P*-value
Leg Raise Rate (/min)	41	13.42 ± 2.84	12.93 ± 2.32	0.135	0.8934
Body Shake Rate (/min)	41	11.14 ± 2.49	12.27 ± 2.14	0.347	0.7305
Time to Court (s)	39	320.72 ± 76.46	117.43 ± 24.98	2.688	0.010*
Courtship Duration (s)	41	799.71 ± 152.68	1033.01 ± 163.47	1.334	0.2010
Copulation Duration (s)	18	860.84 ± 134.27	744.10 ± 107.31	0.135	0.8934

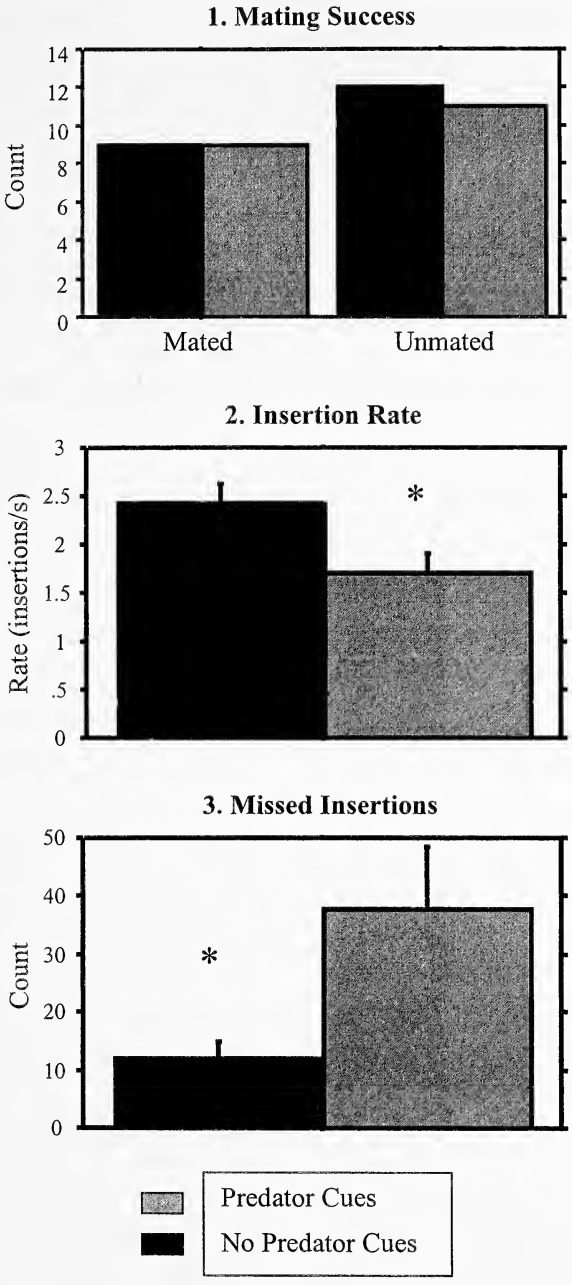
with the female for a thirty minute period. During each trial period we recorded two primary courtship behaviors: leg raises and body shakes (see Montgomery 1903 and Kaston 1936 for a complete description of *P. milvina* courtship behaviors). We also measured (1) time until courtship (the time period from the beginning of the trial to the first body shake or leg raise), (2) courtship duration (the time period from the first body shake or leg raise to a successful mount), (3) time until copulation (the time period from the start of the trial to the first palpal insertion) and (4) copulation duration (the time period from the first palpal insertion to a dismount).

In addition to courtship behaviors and copulation duration, we also measured more specific copulatory behaviors, including the total number of palpal insertions, the rate of palpal insertion per unit of time mounted on the female, and the total number of attempted palpal insertions that failed (general lycosid palpal insertion behavior described in Rovner 1975). For purposes of our study, palpal insertions were recorded as successful only if the extreme proximal end of the hematodocha was observed to visibly expand and the female abdomen concomitantly inflated with this expansion. A palpal insertion was recorded as "failed" only if the pedipalp became decoupled from the epigynum at the time of inflation resulting in the hematodocha expanding external to the female reproductive tract. Because of the difficulty in accurately videotaping copulatory behaviors, all data were recorded live with direct observations using the software package Noldus Observer 4.1®. Each male *P. milvina* was given 30 minutes to mount and begin mating before the trial was terminated. Pairs that were *in copula* after 30 minutes were allowed to continue mating until the male dismounted. Males that failed to mount within the 30 minute period were recorded as unsuccessful. Voucher specimens from this study were deposited in the Museum of Nature and Science, Denver, Colorado.

RESULTS

Most of the conspicuous behaviors exhibited during *P. milvina* courtship displays were not significantly different between treatments (Table 1). The presence of substratum-borne predator cues did not have a significant effect on courtship duration or either measure of courtship intensity (leg raise rates, or body shake rates) (Table 1) but did significantly affect time until courtship (Table 1). In the presence of predator cues, males took more than twice as long to initiate a leg raise or body shake than males without predator cues present (Table 1).

The presence of substratum-borne predator cues did not affect the mating success of *P. milvina* ($X^2 = 0.0191$; $P > 0.90$) (Fig. 1). Mating frequency was 42.8% for the no-predator treatment and 45% for the predator cues treatment. There was also no significant difference in copulation duration between treatments (Table 1). While most courtship behaviors were similar across treatments, we did observe some differences in copulatory behavior. Pedipalp insertion rates were significantly lower for matings under perceived predation risk ($t = 2.620$; $P = 0.0186$; $n = 18$) (Fig. 2), and the number of failed palpal insertions were significantly higher for the predator cues treatment ($t = 2.292$; $P = 0.0358$; $n = 18$) (Fig. 3). The total number of insertions during copulation ranged from a minimum of nine to a maximum of forty (mean = 25.16 ± 2.17 S.E.; $n = 18$) with failed insertion attempts being considerably more variable (range 1–99) (Fig. 3).



Figures 1–3.—1. Male mating success among *P. milvina* pairs with and without *H. helluo* cues present (n = 21 for no predator cues, n = 20 for predator cues). 2. Mean successful palpal insertion and hematodocha inflation rates (± S.E.) into the female epigynum (n = 9/treatment); 3. Total number of failed pedipalp insertions and hematodocha inflations when *H. helluo* cues are present (n = 9/treatment). Asterisks indicate significant differences between predator and no-predator treatments based on a two sample t-test (α = 0.05).

DISCUSSION

Among measured courtship behaviors, only time until the onset of courtship showed a significant difference between treatments. This difference was likely due to a marked reduction in overall activity level by either the male, the female or both when on substrates containing *H. helluo* cues. During our observation of pairs among control treatments, the male would begin localized searching and

chemoexploring immediately after detection of female silk. During this experiment, leg raises and body shakes were observed only after the female had either made some overt movement to draw the male's attention or after the male had made direct physical contact with the female. Males on *H. helluo* cues showed similar behaviors except they exhibited much reduced localized searching and occasionally prolonged periods of immobility. Anecdotally, we observed that females also moved much less frequently on *H. helluo* cues. Although this was not quantified directly in this study, other published studies have consistently documented significant reductions in activity of adult female *P. milvina* when encountering *H. helluo* cues (Persons et al. 2001, 2002; Persons & Rypstra, 2001; Barnes et al. 2002). We believe that reduced female movement rendered them vibratorily and visually cryptic to males and therefore impaired the ability of males to initially perceive females as has been found in other lycosids (Rovner 1996). Male activity could also have been compromised by the presence of *H. helluo* cues. This, in turn, may impair the ability of males to locate female silk or the female directly and delay the onset of courtship. Since we did not directly measure male and female activity in this study, it is difficult to ascertain the extent to which male or female behavior impacts the timing of courtship. Further, it is possible that males could perceive females while under perceived risk to the same degree as males not under risk, but chose to delay courtship because of the possible presence of a predator.

Although the onset of courtship appeared to be affected by *H. helluo* cues, the intensity of male courtship displays and mating success did not differ among treatments. Recent studies have established that male body shake and leg raise rates significantly affect *P. milvina* mating success (Rypstra et al. 2003; Brautigam & Persons 2003) . Since leg raise and body shake rates were the same among treatments, as well as mating success, we can tentatively infer that females do not modify their mate choice criteria with respect to male displays while under risk. It seems likely that males weigh the immediate benefits of mating more highly than the possible predation costs of display. Predator chemical cues, by their nature, only indicate a probability of a predator being in the area rather than confirmation of such a predator. Additional visual or vibratory information about the presence of a predator may be necessary to induce changes in conspicuous components of display that are known to be used in mate choice criteria.

Although predation risk had only a minor impact on courtship behaviors, we found significant differences in important copulatory behaviors. Insertion rates were significantly reduced while under predation risk. Presumably, this was due to a significantly higher number of failed insertions. It remains unclear why failed insertions increased while under risk, however several vertebrate studies indicate that efficiency of complex tasks such as foraging, is compromised by increased predator vigilance (Milinski 1984; Dukas & Kamil 2000, 2001). We suggest that increased predator vigilance during predator encounters may reduce attention paid to complex copulatory maneuvers.

The fitness consequences, if any, of decreased palpal insertion rates are unknown. If sperm is transferred at a similar rate throughout intromission, predation risk may significantly decrease transfer efficiency and possibly limit sperm availability to the female. Alternatively, if most sperm are transferred very early during copulation; as suggested by other spider species (Suter & Parkhill 1990), reduced insertion rates and missed insertions may have a minimal impact on male or female fitness. However, even if all sperm is transferred during the first insertion, continued insertions may still be adaptive. Prolonged intromission by males may serve as a form of copulatory courtship by providing information to the female about body condition, genetic quality, or otherwise serving to convince the female to accept the male's sperm. Continued intromission may also serve as a form of mate guarding, allowing sufficient time for the sperm to capacitate (reviewed in Eberhard 1996). As suggested by Suter and Parkhill (1990), further copulation may function to transfer substances in the ejaculate that may facilitate oviposition or nourish the offspring.

Our results suggest that predation risk may have the greatest impact on mate searching and copulation rather than courtship displays. As such, our study underscores the need to examine not only how conspicuous displays are influenced by predators, but also how cop-

ulatory behavior itself is affected. Future studies should address the reproductive consequences of modifed copulatory behavior while under predation risk.

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WEB ORIENTATION, STABILIMENTUM STRUCTURE AND PREDATORY BEHAVIOR OF *ARGIOPE FLORIDA* CHAMBERLIN & IVIE 1944 (ARANEAE, ARANEIDAE, ARGIOPINAE)

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ABSTRACT. This study was undertaken to describe the web orientation, stabilimentum structure and predatory behavior of *Argiope florida* Chamberlin & Ivie 1944 (Araneae, Araneidae, Argiopinae), a virtually unstudied orb-web spider of the southeastern United States. Adult female *Argiope florida* were sampled from five sandy ridge areas of Florida. Compass orientation of the spider's dorsum, incline of the web from vertical and hub height were measured. The presence of male *A. florida*, barrier webs, kleptoparasitic species of *Argyrodes* Simon 1864 (Araneae, Theridiidae), wrapped prey and large areas of web damage were noted. Predatory behavior was elicited by touching a radius with a 100 Hz tuning fork. The number of stabilimentum arms was measured, along with their arrangement, length and number of silk bands. On average, webs faced 100° E of N, were inclined 19° from vertical and were 1 m from the ground at the hub. Responses to the tuning fork, which closely resembled the responses to actual prey, were more vigorous when *Argyrodes* spp. were present on the web, but were not different when wrapped prey were present on the web. Most webs had stabilimenta and most stabilimenta had four arms in a cruciate pattern. The upper arms tended to be smaller and spaced further apart than the lower arms. Spider size was related to the angle between the lower arms of the stabilimentum, but not to other measures of the stabilimentum.

Keywords: Orb web, prey capture, Florida scrub, tuning fork, *Argyrodes* kleptoparasites

The behavior of orb-web spiders has long been a topic of interest. Much of the research has focused on the building of the web and the variables that affect its final structure, especially its size, asymmetry, number of radii and distance between loops of the sticky spiral (e.g., Craig 1987; Sandoval 1994; Sherman 1994; McReynolds 2000; Venner et al. 2000). Other behavioral research has been dedicated to web site selection (e.g., Enders 1973, 1976), compass orientation (e.g., Carrel 1978; Tolbert 1979; Biere & Uetz 1981; Caine & Heiber 1987), sexual behavior (e.g., Elgar et al. 2000), thermoregulatory posturing (e.g., Humphreys 1991; Higgins & Ezcurra 1996), predatory behavior (e.g., Robinson & Robinson 1974; Klärner & Barth 1982; Masters & Moffat 1983; Masters 1984) and the effects of kleptoparasitic *Argyrodes* spp. Simon, 1864 (Araneae, Theridiidae; e.g., Larcher & Wise 1985; Elgar 1989; Cangialosi 1990).

Many orb-web spiders add bits of debris, egg cases, or conspicuous tufts or bands of silk to the frame, radii and/or hub of their webs. This web-decorating behavior is seen in a number of Araneidae, spanning 15 genera and occurring in both ecribellate and cribellate spiders (Scharff & Coddington 1997). A phylogenetic analysis of this family by Scharff & Coddington (1997) suggests that web-decorating behavior has evolved nine separate times in Araneidae. The extent to which web-decorating behavior has established itself in the Araneidae suggests that this behavior serves

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an important function(s) in spiders that build orb webs.

Spiders in the genus *Argiope* Audouin 1826 often decorate their nearly invisible orb webs with conspicuous zigzags of silk called stabilimenta. However, the ecological function of stabilimentum building is still unresolved (see Herberstein et al. 2000a). Because of its reflectivity in both the visible and ultraviolet (UV) regions of the spectrum (Craig & Bernard 1990, Watanabe 1999, Zschokke 2002), many authors have suggested that the stabilimentum is used as a visual signal. However, it is much debated whether the primary recipients of this signal are predators, prey or megafauna. Arguments that the primary recipients are predators suggest the stabilimentum thwarts predators by displacing attacks or changing the apparent size or shape of the spider (Hingston 1927; Ewer 1972; Eberhard 1973; Horton 1980; Edmunds 1986; Schoener & Spiller 1992). Arguments that the primary recipients are prey center around the UV reflectivity of the stabilimentum, which may attract insects by simulating flowers or patches of daylight in vegetation (Craig & Bernard 1990; Craig 1991; Tso 1996; Hauber 1998; Tso 1998a, 1998b; Watanabe 1999; Herberstein 2000; but see Blackledge & Wenzel 1999, 2000). Finally, the stabilimentum may signal the presence of the orb to megafauna that may otherwise walk or fly through it; this is mutually beneficial because the spider keeps its web intact and the megafauna do not have to groom the sticky spiral (Eisner & Nowicki 1983; Eberhard 1990; Kerr 1993; Blackledge & Wenzel 1999). In any case, the effectiveness of a visual signal is in part a function of the light that strikes it, which in any season would be affected by the web's compass direction and angle from vertical. However, this basic natural history information is often missing, even for some of the best-studied species. Indeed, many species are virtually unstudied beyond their description and classification.

One of the relatively unknown species is *Argiope florida* Chamberlin & Ivie 1944. In the most recent description and classification of this species, Levi (1968) summarizes the little that is known of its natural history: adults range from central North Carolina south to the panhandle and peninsula of Florida, mature from July to November and build a cruciate stabilimentum. In Florida, the species lives in sand scrub and pine flatwoods. The only other study mentioning the species is that of Eisner & Nowicki (1983), who noted that removing the stabilimentum did not seem to affect prey capture or evasive behaviors. The purpose of the present study was to further characterize the web and stabilimentum of *A. florida*, to gather baseline data on predatory behavior via responses to a tuning fork and examine any interesting relationships that were revealed.

METHODS

Numerous areas of the Florida panhandle, peninsula and keys were visited during 2000–2002 and locations where *A. florida* were found are summarized in Table 1. A search for adult female *Argiope* was carried out by walking through the habitat during the daytime and scanning the vegetation from the ground to a height of about 2.5 m. *Argiope florida* hang head down at the hub on the underside of their slightly tilted webs all day, like its congenerics (Comstock 1948). Upon locating an individual, the date, time, location, temperature and weather were noted.

Next, two measures of the web were taken from a distance of about 1–3 m, with careful effort to avoid disturbing the spider. The compass direction its dorsum faced was recorded to the nearest 5°. The angle of the plane of the web was measured with a clinometer and recorded to the nearest 1° from vertical. Sometimes the web was significantly flexed at the hub, so that the incline of the web above the hub was quite different from that below the hub. In these situations, the incline of a line connecting the tips of the spider's 4th legs to the tips of its 1st legs was used.

Several measures were then taken from a distance of less than 1 m, again being careful to avoid disturbing the spider. First, it was noted whether any large sections of the web were missing or damaged. Then, both sides of the web were inspected for the presence of barrier webs, which are cobweb-like tangles of non-sticky silk placed adjacent to the orb. Next, the orb and barrier webs were carefully searched for male *A. florida* and the kleptoparasitic *Argyrodes* spp. (the frame threads and nearby vegetation were not searched for males or *Argyrodes* spp.). Lastly, the presence of wrapped prey was noted.

Table 1.—Dates and locations where *A. florida* were found. SP = State Park, NF = National Forest, SF = State Forest, CO = County.

n	Ridge	Locality and/or Landmark, County	Latitude/Longitude	Dates Found
9	Atlantic Coastal	Jonathan Dickinson SP, Hobe Sound, Martin CO	27°01′01″N 80°06′37″W	31 Aug 2001 17 Oct 2001 05 Oct 2002
1	Bell	Bell, Gilchrist CO	29°47′25″N 82°51′13″W	15 Oct 2001
38	Lake Wales	Archbold Biological Station, Highlands CO	27°10′55″N 81°21′08″W	15–17 Sep 2001 19 Oct 2001 15 Aug 2002 13 Sep 2002
3	Lake Wales	Hickory Lake Scrub, Polk CO	27°41′47″N 81°32′23″W	03 Sep 2001
4	Lake Wales	Sun 'N Lake, Lake Placid, Highlands CO	27°14′55″N 81°18′02″W	02 Aug 2002
6	Mount Dora	Alexander Springs, Ocala NF, Lake CO	29°07′24″N 81°34′40″W	02 Sep 2001
1	Mount Dora	Healing Waters, Ocala NF, Lake CO	29°10′14″N 81°38′14″W	02 Sep 2001
1	Unnamed	Camel Lake, Appalachicola SF, Liberty CO	30°06′30″N 84°58′51″W	14 Oct 2001
1	Unnamed	Pine Log SF, Panama City, Bay CO	30°24′18″N 85°52′06″W	14 Oct 2001

A predatory response was then elicited by touching the web with a 100 Hz tuning fork. In controlled experiments, 100 Hz vibrations increased at the hub of empty *Larinioides sclopetarius* (Clerck 1757) orbs when flies (*Calliphora erythrocephala*), mosquitoes (*Culex* spp.) and bees (*Apis mellifora*) began buzzing while trying to free themselves (Masters 1984). Tuning forks produce pure tones at an initial amplitude of 100–110 dB (reference 0.0002 dynes/cm^2), which rapidly decay (Frings & Frings 1966). Amplitude is thus difficult to control with tuning forks, but natural prey produce a very wide range of amplitudes (Barrows 1915; Landolfa & Barth 1996). Pilot work and previous research (Boys 1880; Wells 1936; Frings & Frings 1966) revealed that striking the tuning fork near the spider can produce a number of behavioral responses without even touching the web, probably due to the significant near-field air vibrations of a tuning fork. For this research, the tuning fork was struck at least 1 m from the spider and not passed near the spider before touching the web. Five seconds after striking the fork, a single tine of the fork was gently pressed onto a radius at a 45° angle. This angle should produce a high amplitude (about 2 mm) combination of transverse and longitudinal vibrations, which are believed to be important for prey detection, localization and recognition (Masters & Markl 1981; Klärner & Barth 1982; Masters 1984). The stimulated radius was to the right or left of the hub, approximately halfway from the hub to the edge of the orb (typically 15–25 cm from the hub). The radius was pushed in about 1.5 cm with the tine for about 3 s and then allowed to return to its original position. The fork was left in place about 10–15 s.

Pilot testing revealed that tuning fork stimulation of other areas of the web was less satisfactory. Stimulation above the hub was difficult because this area of web was often small, and the response may be inhibited by having to rotate 180° and climb upward (cf. Masters & Moffat 1983). Stimulation below the hub did not allow for an assessment of rotation of the body toward the stimulus, an important element of the response (Boys 1880), and could potentially confuse an attack with an escape-drop. Stimulation of the frame threads often produces a vigorous response (Boys 1880; pers. obs.), but prey items are not typically caught there.

Predatory responses were easily scored

from no response at all (=0.0) to exhibiting the full range of behaviors that a real prey item would elicit (=5.0). The following are listed from least to most vigorous response, and were scored as numbered: 1) moving a leg, typically to place a tarsus on or near the radius being stimulated, 2) rotating the body so that the axis of the cephalothorax and abdomen is aligned with the point of stimulation, 3) plucking or tugging on radii, 4) approaching the fork and making physical contact with it, usually with the 1st and 2nd tarsi (if the approach were interrupted by stopping or returning to the hub, 0.5 points were deducted from the score) and 5) wrapping the tip of one or both tines with silk. Thus, a spider that quickly rotated, approached and wrapped the fork with silk scored 5.0. A spider that paused during the approach but ultimately wrapped the fork with silk scored 4.5. A spider that rotated but never approached scored 2.0. Spiders that bit the fork consistently did so after wrapping, but this behavior was not factored into their predatory response score because the 10–15 s that the tuning fork was in the web may not have been sufficient time for a full predatory response if an individual spent several seconds wrapping a large area of the fork. An avoidance response such as dropping off the web or moving away from the fork was rare.

The remaining measures were taken last because they required close proximity to the spider and often caused the spider to leave the hub. The height of the hub above ground was measured with an extension rule. The number and pattern of stabilimentum arms was noted, after which three measures were taken on each arm: 1) its length, measured with dial calipers, 2) the number of bands of silk crossing from one radius to another (hereafter "bands") and 3) the angle it formed with the next arm, measured with a transparent goniometer. Next, dial calipers were used to obtain an index of size from leg #2. Specifically, the chord of the distance from the proximal end of the metatarsus to the distal tip of the tarsus was measured. Although there may be some flexion at the tarsometatarsal joint, this chord was very close on average to the sum of Levi's (1968) averages for the tarsal and metatarsal lengths.

After these data were collected in the field, the azimuth of the sun at the dawn of the day was obtained to the nearest 0.1° from the U. S. Naval Observatory's Astronomical Applications Department (http://aa.usno.navy.mil/). Statistics involving angles were calculated using the methods described by Mardia (1972), Batschelet (1981) and Zar (1996). Sample sizes vary because some measures were added after some data collection had taken place, and not all measures could be taken successfully on all spiders. Voucher specimens of *A. florida* and *Argyrodes* spp. are deposited in the arthropod collection at the Archbold Biological Station in Lake Placid, Florida.

RESULTS

Argiope florida were only found between August and October in the sand scrub and sandhill habitats of the Florida ridges. Specifically, *A. florida* were found on the Atlantic Coastal Ridge (n = 9), the Bell Ridge (n = 1), the Lake Wales Ridge (n = 45), the Mount Dora Ridge (n = 7) and in unnamed ridge areas in the panhandle (n = 2) (see Table 1). *Argiope florida* and *A. aurantia* Lucas 1833 were frequently sympatric on the ridges, even though *A. aurantia* is often found in wetter habitats such as lake margins and swamps. There was no obvious horizontal or other niche separation between *A. florida* and *A. aurantia*; in fact, their webs were often close together, and occasionally in clusters with both species present. *Argiope florida* were not found south of Martin County, and thus their distribution did not overlap that of the *Argiope argentata* (Fabricius 1775) commonly found in southern peninsular Florida and the keys. All *Argiope* spp. in Florida are easily recognizable by shape and color patterns; also, *A. florida* and *A. argentata* construct cruciate stabilimenta, whereas *A. aurantia* construct linear stabilimenta.

During data collection, temperature ranged from 21–38°C and was typically about 30–35°C. Spiders were frequently observed with their abdomens flexed away from the orb or off to the side, presumably to minimize exposure to the sun. Webs were never observed to be vertical, but instead were inclined by a mean $\bar{\phi}$ = 18.7°, s = 8.9° (n = 63). Twenty percent (n = 13 of 64 webs examined) had large sections of the web missing or damaged. Some of these were excluded from further measures and later analyses as appropriate. Twenty-five percent had barrier webs (n = 12

of 48 examined); barrier webs were occasionally on both sides of the orb, but usually only on the same side as the spider. No male *A. florida* were found on $n = 48$ webs searched. *Argyrodes* spp. were present on 8 (42%) of $n = 19$ webs searched (range 1–4 individuals per web). Individual *Argyrodes* were not identified to species. Fourteen of 49 webs searched (29%) had wrapped prey present either in the sticky spiral, at the hub, or at the spider's mouth. The height of the hub above the ground was measured on $n = 48$ webs and varied from 0.43 m to 1.61 m ($\bar{x} = 1.06$, $s = 0.28$). Although genitalia were not inspected, all were likely adults or at least subadults based on size: the chord of the tarsus + metatarsus on leg II averaged 10.9 mm ($n = 61$, $s = 1.1$, Min = 7.0, Max = 13.3).

The sampled *A. florida* showed a significant tendency to orient the plane of their webs parallel to the N-S axis so that their dorsa faced E or W. Using the direction the dorsum faced (*mod* 180°), the mean ± *s* compass direction was $\bar{\phi} = 99.6° \pm 52.6°$ E of N (95% CI = 83.6°–115.6°). With $n = 64$, the Rayleigh test for directional preference was significant (mean vector length $r = 0.58$, $P < 0.001$). On the days of data collection, the sun's azimuth at dawn ranged from 69.6°–101.1° E of N. However, the orientation of the web did not correlate with the dawn azimuth ($r = 0.24$, $n = 64$, $P > 0.40$).

The 100Hz tuning fork was applied to $n = 61$ webs. Thirty-seven spiders approached the fork and wrapped it in silk (score = 4.5 for $n = 17$ that paused on the way and 5.0 for $n = 20$ that did not). Ten spiders approached but did not wrap the fork (score 3.5 for $n = 7$ and 4.0 for $n = 3$). Five spiders moved a leg but nothing more (score = 1.0). Nine spiders did not respond at all (score = 0.0). Overall, the mean ± *s* response to $n = 61$ stimulations was 3.57 ± 1.84. Mean predatory responses were not different when wrapped prey were present ($\bar{x} = 3.27$, $s = 1.99$, $n = 13$) *vs.* absent ($\bar{x} = 3.92$, $s = 1.62$, $n = 33$; equal variances $t = 1.16$, $df = 44$, two-tailed $P = 0.25$). However, predatory responses were stronger and less variable when *Argyrodes* were present ($\bar{x} = 4.86$, $s = 0.24$, $n = 7$) *vs.* absent ($\bar{x} = 3.40$, $s = 2.16$, $n = 10$); the variance difference was significant ($F = 78.21$, $df = 9, 6$, $P < 0.0001$) and the mean difference was nearly significant (unequal variances $t = 2.11$, $df = 9$, two-tailed $P = 0.06$).

Most webs had a four-arm, cruciate stabilimentum, but other patterns were observed (Fig. 1). Descriptive statistics on the stabilimentum measures are given in Table 2. Paired difference tests were used to compare lower arms and upper arms on the same web. Lower arms were closer together than upper arms (Hotelling's $F = 3.66$, $df = 2, 25$, $P = 0.040$). Lower arms were longer ($t = 8.00$, $df = 46$, two-tailed $P \ll 0.0001$), but there was no difference between lower and upper arms in their length asymmetry ($t = 0.37$, $df = 30$, two-tailed $P = 0.716$). Lower arms had more bands ($t = 10.07$, $df = 46$, $P \ll 0.0001$), but there was no difference between lower and upper arms in the number of bands per cm arm length ($t = 0.40$, $df = 46$, two-tailed $P = 0.691$). Given that length would be added to an arm by adding more bands, the amount of variation in length explained by bands was surprisingly low: for $n = 46$ upper arms, $r^2 = 0.49$ and for $n = 56$ lower arms, $r^2 = 0.63$ (for these calculations, one arm was chosen at random from stabilimenta with more than one upper or lower arm). This suggests that other factors play a significant role in the spacing between bands.

The size index was not related to the total number of bands ($r = +0.07$, $n = 55$, $P = 0.61$), the total length of the arms of the stabilimentum ($r = +0.12$, $n = 55$, $P = 0.38$), the bands/cm in the stabilimentum arms ($r = -0.19$, $n = 55$, $P = 0.16$), or the angle between the two lower arms of the stabilimentum ($r = +0.12$, $n = 32$, $P = 0.51$). The size index was related, however, to the angle between the two upper arms of the stabilimentum ($r = +0.41$, $n = 25$, $P = 0.04$).

DISCUSSION

Areas where *Argiope* spp. were found correspond fairly well with the distribution maps of Levi (1968) with two exceptions. First, Levi (1968) found *A. florida* on the Atlantic Coastal Ridge south of Martin County, whereas they were not found in these areas in the present study. This may be due to a reduction in sand scrub habitat in these areas (Myers 1990). Second, based on collecting reports with habitat information, Levi (1968) states that *A. aurantia* in Florida are found "rarely in sand scrub", whereas they were easily

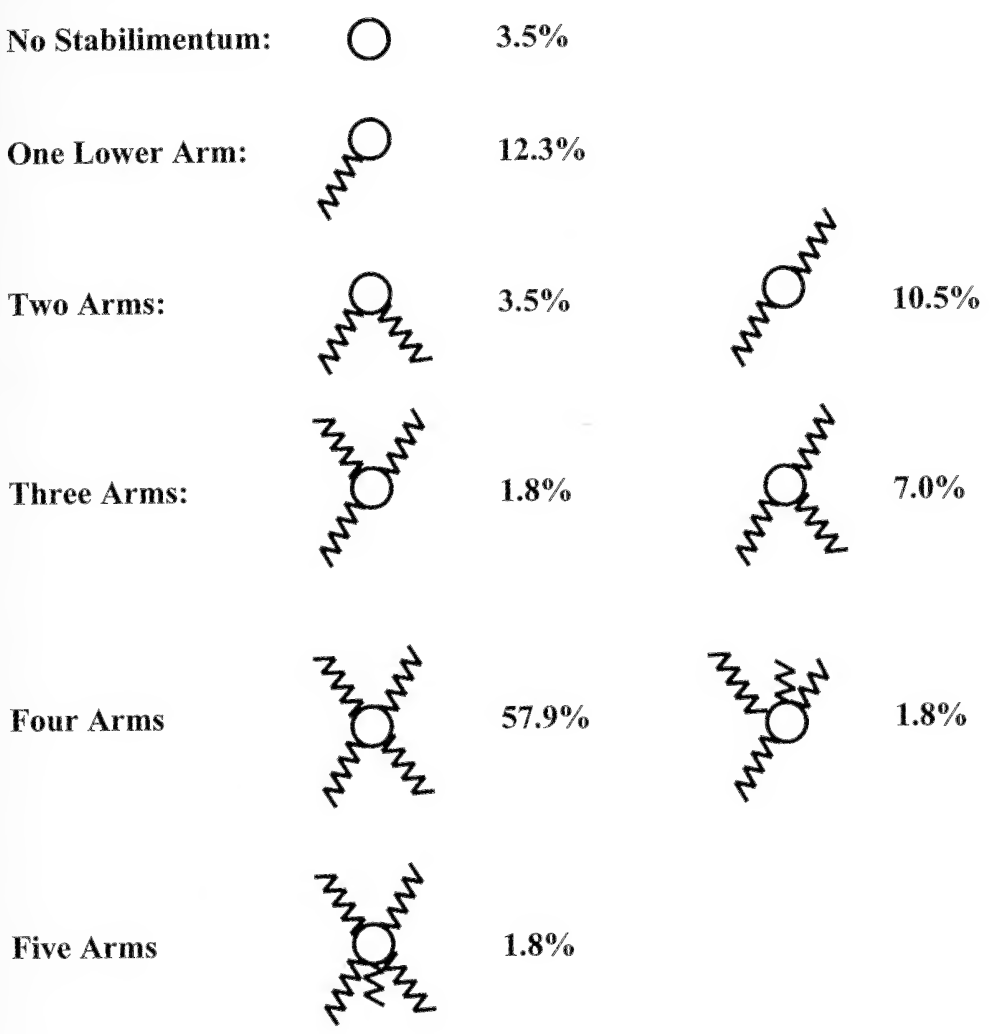

Figure 1.—Observed patterns of stabilimentum structure and their frequencies. Percentages are based on $n = 57$ webs.

found and quite numerous in sand scrub in the present study. Of course, the collecting reports and present authors may be defining "sand scrub" quite differently.

In open habitat with highly reflective sand, at subtropical latitudes, and at the hottest times of the year, *A. florida* hang at the hub of fairly exposed webs with their dorsa facing due east/west on average. It may be worthwhile to examine the behavioral and physiological responses to the heat load that could result from this combination of temperature, exposure and orientation. Orb-web spiders with webs in open areas can regulate insolation (and thus heat load) by retreating to shade at high temperatures, posturing their bodies to adjust exposed surface area (i.e., Pointing 1965; Suter 1981), orienting their webs in a particular compass direction (i.e., Carrel 1978; Biere & Uetz 1981; Caine & Heiber 1987), building reflective silk shields over the hub (Humphreys 1992), and/or reflecting light with hairs on the cephalothorax and abdomen (Robinson & Robinson 1978). *Argiope florida* orbs are parallel to the N-S axis, which on nearly vertical webs would seem to maximize exposure to the sun. *Argiope* do not use retreats (Levi 1968; Tolbert 1979), and their stabilimenta do not cross the hub and thus do not provide a sun shield. Thermoregulation in *A.*

Table 2.—Descriptive statistics on stabilimentum characteristics. Sample sizes refer to number of spiders. If a web had two upper arms, their measures were averaged and the averages were used in the analyses. If a spider had built only one upper arm or only one lower arm, the length of this arm was used but this spider could not contribute to the analyses of asymmetry and angle. Analyses of the angle between upper and lower arms required an upper arm and a lower arm on the same side of the hub.

Variable	*n*	Mean	*s*	Min	Max
Angle Between the Upper Arms	27	68.8°	10.3°	46°	87°
Angle Between the Lower Arms	34	60.2°	13.9°	24°	95°
Length of the Upper Arms (cm)	47	1.18	0.73	0.41	4.32
Length of the Lower Arms (cm)	56	2.04	1.09	0.54	6.29
Asymmetry in the Length of the Upper Arms (cm)	34	0.47	0.54	0.01	2.71
Asymmetry in the Length of the Lower Arms (cm)	40	0.52	0.47	0.04	1.84
Bands in the Upper Arms	47	4.78	2.23	1	12
Bands in the Lower Arms	56	8.96	4.25	2	18
Bands/cm in the Upper Arms	47	4.77	2.27	0.98	11.43
Bands/cm in the Lower Arms	56	4.72	1.47	1.45	8.38
Angle Between the Upper and Lower Arms	32	112.2°	8.9°	90°	139°
Asymmetry in the Angle Between the Upper and Lower Arms	27	10.0°	7.1°	0°	27°

florida, therefore, would seem to come from behavioral posturing and silvery reflective hairs covering the dorsal cephalothorax and partially covering the dorsal abdomen (cf. Tolbert 1979).

While heat load may be a cost of the placement of their webs, benefits may come from an increase in prey capture and/or a decrease in the frequency of web loss. A large proportion (29%) of webs were found with wrapped prey already in the spiral, at the hub, or at the spider's mouth. Also, a large number of prey impacts probably accounts for the large proportion of webs found with sections damaged or missing. As discussed above, the stabilimentum may increase benefits by attracting prey and/or preventing megafauna from destroying the web. Both of these functions require reflection of light from the stabilimentum; habitat selection, compass direction of the web, and incline of the web from vertical will influence the maximum amount and timing of insolation. Thus, the E-W direction and the 19° incline may be a combination that optimizes reflection of light from the stabilimentum for prey capture and web protection in this habitat.

Barrier webs may not generally be worth their costs for *A. florida*. After comparing three populations of *A. argentata* in the Galapagos, Lubin (1975) suggested that barrier webs help to mechanically strengthen the web because they were more frequent in areas of high wind. The percentage of webs with a barrier web in a low-wind area (28%) closely matched that of the *A. florida* in the present study (25%); both were much lower than the high-wind areas (68%). It is possible that *A. florida* webs do not need the mechanical stability of a barrier web. Also, if the stabilimentum is serving to deter larger animals from walking or flying through the web, the early warning provided by a barrier web may be superfluous enough to not justify the cost of the additional silk. The barrier web also provides a habitat for kleptoparasitic *Argyrodes* spp. By living in the barrier web, *Argyrodes* spp. likely can detect, through vibrations, when a prey item has been captured and wrapped; further, by not living on the orb, the threat of being depredated by the host is reduced (Vollrath 1979). On the other hand, barrier webs may benefit the host by deterring or warning of hymenopteran predators or parasites (Tolbert 1975).

The tuning fork stimulation elicited naturalistic predatory responses. Specifically, the sequence of observed responses closely follow the sequences described by (1) Frings & Frings (1966) for 20–160 Hz stimulation with a modified audio-oscillator in the webs of *A. aurantia*, (2) Robinson & Olizarri (1971) for heavy prey with sustained vibrations in the web of *A. argentata*, (3) Harwood (1974) for large, active, non-lepidopteran prey in the web of *A. aurantia*, (4) Robinson & Robinson

(1974) for orthopterans in the webs of *Argiope picta* L. Koch 1871, *Argiope aemula* (Walckenaer 1842) and *Argiope reinwardti* (Doleschall 1859), and (5) Olive (1980) for slowly escaping, large acridid orthopterans in the webs of *A. trifasciata*. Thus, naturalistic responses can be obtained in the field without having to transport electronic equipment or live prey. Live prey items placed on webs are also likely to be more variable in stimulation than a tuning fork.

The response to the tuning fork was usually vigorous. Almost 80% of the tested spiders approached and touched the fork, and over 60% wrapped it in silk. This sequence of predatory behavior was unaffected by recent prey capture; the response to the tuning fork was not different when wrapped prey were already present in the web. This is consistent with the arguments set out in Wise (1993) that spiders may be food-limited in general; each additional prey item can further increase survival and fecundity. It may be that spiders with kleptoparasitic *Argyrodes* spp. in their webs had higher and more consistent predatory response scores because some proportion of their captured prey is stolen, reducing their total consumption (cf. Rypstra 1981).

Argiope florida stabilimenta were remarkable in four ways. First, 13 other species of *Argiope* are known to add cruciate stabilimenta to their webs, but these often comprise only a couple of arms, with full crosses usually being relatively rare (Hingston 1927; Yaginuma 1960; Levi 1968; Marples 1969; Robinson & Robinson 1970, 1974; Lubin 1975; Robinson & Lubin 1979; Robinson & Robinson 1980; Edmunds 1986; Nentwig & Heimer 1987; Nentwig & Rogg 1988; Kerr 1993; Elgar et al. 1996; Hauber 1998; Herberstein et al. 2000b). In comparison, *A. florida* has a relatively high proportion of webs with a complete cross (almost 60%). Second, Hingston (1927) remarked that the four arms in the cruciate stabilimentum of *Argiope pulchella* Thorell, 1881 were "evenly separated. . . at equidistant points". This is a very different arrangement from *A. florida* stabilimenta, in which the upper and lower pairs of arms are each separated by about 65°. No other studies have quantified the angular arrangement of the arms in *Argiope* cruciate stabilimenta. Third, there were a substantial number of differences between the upper and lower arms of *A. florida* stabilimenta. While this may be related to the function of the stabilimentum, it may also be reflective of the asymmetry in the orb itself: the area above the hub is almost always smaller than the area below the hub. It would be interesting to know how closely stabilimentum asymmetry is related to the structural asymmetries of the orb itself. It may be relevant that size was related to the angle between the upper arms but not to the angle between the lower arms, because size is known to contribute to asymmetries in orb webs (Herberstein & Heiling 1999). Fourth, the number of bands is sufficiently independent of the length of the stabilimentum arm to continue separate consideration. Arms of the same length can show considerable differences in the number, thickness, spacing, silk density, and even pattern of the bands (personal observations). For example, Hingston (1927) counted an average of 6.3 bands/cm on the linear stabilimenta of *Argiope sector* (Forskål, 1775), over 30% more dense than the bands of *A. florida* in the present study.

Further research into the distribution, natural history and behavior of *A. florida* could make valuable contributions to conservation and behavioral biology. A phenology of the presence of males and reproductive behavior of the species is needed. Also, the few patches of sand scrub remaining in Palm Beach, Broward and Dade Counties should be checked for the presence of *A. florida*. Behavioral research on *A. florida* could facilitate and extend comparative work with its more extensively studied congeners. If the stabilimentum is a visual signal, there may well be costs or benefits for spiders that deviate from the mean on web orientation from vertical and compass direction of the plane of the orb. If variability in these characters can account for variability in prey capture success and/or web destruction, this would speak to general theories of stabilimentum function. Investigations into the influence of *Argyrodes* kleptoparasitism on *Argiope* behavior should be pursued. A cost-benefit analysis of barrier web construction that considers *Argyrodes* kleptoparasitism and hymenopteran attacks could be used to address the finding that 25% of *A. florida* built barrier webs. Also, changes in the extent of kleptoparasitism should be related to changes in predatory behavior; the exact nature of this relationship, including *Argyrodes* depredation

by *Argiope*, should be quantified. Lastly, variation in the number of arms in the stabilimentum, the spacing or arrangement of arms and band density within arms could all be related to several proposed functions of the stabilimentum and should be considered in future studies of stabilimentum structure and function.

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FIRST FOSSIL FILISTATIDAE: A NEW SPECIES OF *MISIONELLA* IN MIOCENE AMBER FROM THE DOMINICAN REPUBLIC

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ABSTRACT. *Misionella didicostae* new species is described from 15–20 Ma Miocene amber from the Dominican Republic as the first fossil record of the family Filistatidae. The biogeography of the extant (Brazil and Argentina) and the new fossil species supports the hypothesis that the developing northern Greater Antilles and northwestern South America were briefly (33–35 Ma) connected by a landspan centered on the emergent Aves Ridge. Undiscovered extant species of *Misionella* may exist on Hispaniola. The autospasized first pair of legs suggest that the spider was engulfed in a flowing resin seep of relatively low viscosity, rather than having wandered onto a sticky exudate, becoming stuck and then covered by a subsequent resin flow.

Keywords: Hispaniola, Araneae, spider, biogeography, autospasy

The spider family Filistatidae has an almost worldwide distribution in tropical and warm temperate regions, and consists of 107 species and one subspecies in 16 genera (Platnick 2003). These small to medium-sized, cribellate spiders represent one of the most basal branches of the Haplogynae (Platnick et al. 1991). Filistatidae have not previously been described in the fossil record, although Eskov (1990) mentioned a fossil specimen from the Upper Jurassic of Kazakhstan. The current evolutionary tree (including the new fossil described in this paper) of the Haplogynae (Fig. 1) predicts the presence of Filistatidae in the fossil record back to the Upper Cretaceous. However, this is a youngest age prediction based on the presence of Oonopidae and Segestriidae in amber from New Jersey (Penney 2002a, 2004). Here, the first fossil Filistatidae is described in the genus *Misionella*, from Miocene (15–20 Ma; e.g. Iturralde-Vinent & MacPhee 1996) Dominican Republic amber.

METHODS

Preservation.—The spider is preserved close to the surface of a clear yellow, tear-shaped piece of Dominican Republic amber 4 cm long × 1.7 cm wide; for details of locality and stratigraphy see Iturralde-Vinent & MacPhee (1996). The spider is best observed in ventral view. There are two partial insect legs and the associated thoracic sternite in the amber as a syninclusion. The holotype and only known specimen is held in the collection of the Museo del Ámbar Dominicano, Puerto Plata, Dominican Republic.

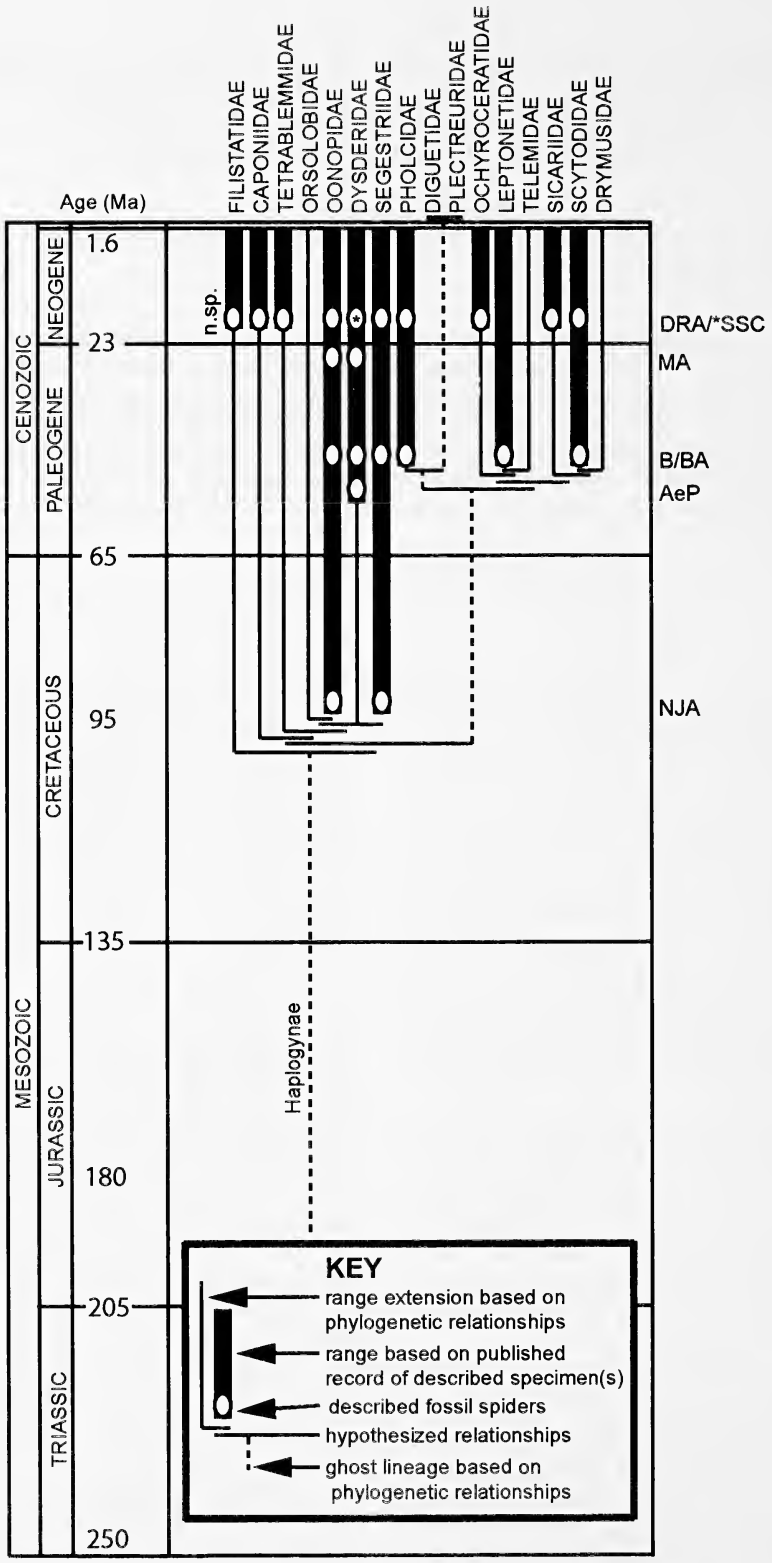
Measurements and drawings.—All measurements were made using an ocular graticule and are in mm. Drawings were done under incident light with a camera lucida attached to an Olympus SZH stereomicroscope and photographs were taken with a Nikon D1X digital camera attached to a Wild M8 stereomicroscope then manipulated in Adobe Photoshop.

Abbreviations used in the text and figures.—In the leg formula (e.g. 1423), the legs are ranked in order of length (longest first). Abbreviations are as follows: cx = coxa; cy = cymbium; e = embolus; fe = femur; h = haemolymph; la = labium; mt = metatarsus; op = opisthosoma; pa = patella; pl = paraembolic lamina; pnm = leg segment present but not measurable; pp = pedipalp; rex = retrolateral excavation; s = long setae; sp = spine; spr = spinneret region; st = sternum; ta = tarsus; ti = tibia; 1–4 = walking legs 1–4.

SYSTEMATIC PALEONTOLOGY

Family Filistatidae Ausserer 1867
Subfamily Prithinae Gray 1995
Misionella Ramírez & Grismado 1997

Type species.—*Filistata mendensis* Mello-Leitão 1920 by original designation.


FILISTATIDAE
CAPONIIDAE
TETRABLEMMIDAE
ORSOLOBIDAE
OONOPIDAE
DYSDERIDAE
SEGESTRIIDAE
PHOLCIDAE
DIGUETIDAE
PLECTREURIDAE
OCHYROCERATIDAE
LEPTONETIDAE
TELEMIDAE
SICARIIDAE
SCYTODIDAE
DRYMUSIDAE
Age (Ma)
CENOZOIC
MESOZOIC
NEOGENE
PALEOGENE
CRETACEOUS
JURASSIC
TRIASSIC
1.6
23
65
95
135
180
205
250
n.sp.
DRA/*SSC
MA
B/BA
AeP
NJA
Haplogynae
KEY
range extension based on phylogenetic relationships
range based on published record of described specimen(s)
described fossil spiders
hypothesized relationships
ghost lineage based on phylogenetic relationships

Distribution.—Recent species in Brazil and Argentina, fossil species in Dominican Republic amber.

Remarks.—*Misionella* was erected as a monotypic genus by Ramírez & Grismado (1997) for *Filistata mendensis* from Brazil and Argentina. Grismado & Ramírez (2000) described a second species from Brazil.

Misionella didicostae new species
Figs. 2–5

Material examined.—Holotype, adult male in Dominican Republic amber, held in the Museo del Ámbar Dominicano, Puerto Plata, Dominican Republic.

Diagnosis.—*Misionella didicostae* can be distinguished from the two known extant species by having a spiralled embolus distally extending well beyond the paraembolic lamina. In addition, it lacks small spinules in the retrolateral excavation of metatarsus 2.

Etymology.—The specific epithet is a matronym in honor of Mrs Ada (Didi) Benelli Costa who co-founded the Museo del Ámbar Dominicano, Puerto Plata, Dominican Republic in 1982, based on collections amassed over 33 years.

Description of holotype.—Body length 2.21; carapace 0.84 long, width not measurable; ocular region slightly raised, with eight closely grouped eyes. Clear views of the eye arrangement and carapace shape are not afforded by the specimen, but there are no obvious differences between the details visible and the figure of the type species provided by Ramírez & Grismado (1997: fig. 96). Only distal tips of chelicerae visible: weak, unmodified with a small fang. Labium longer than broad, with curved sides converging to form a pointed tip; fused to sternum. Maxillae longer than wide, convergent. Sternum subcircular, width 0.40, length of fused sternum and labium 0.77. Opisthosoma 1.21 long, 0.54 wide, fine detail of anal tubercle, spinnerets and cribellum not clear, situated ventrally, advanced from the posterior margin (Figs. 2, 3).

Leg formula 1423; leg 1 cx 0.33, fe 1.86, ti 2.13, mt 1.64, ta 1.00; leg 2 cx 0.30, fe 1.34, ti 1.47, mt 0.70, ta 0.60; leg 3 cx 0.30, fe 0.93, ti 0.93, mt 0.83, ta 0.43; leg 4 cx 0.33, fe 1.36, ti pnm, mt 1.00, ta not preserved; mt 2 with a retrolateral excavation in the distal half bearing a single prominent retrolateral spine (Figs. 2–4); mt 1 with a single long, ventral terminal spine; remaining leg segments without spines. All leg segments, opisthosoma and sternum with clearly visible, long setae. Pedipalp fe long, ti globose without projections, cymbium vestigial and partially fused to tegulum, embolus spirally twisted distally which extends well beyond the paraembolic lamina (Fig. 5).

Female.—Unknown.

Distribution and age.—Dominican Republic amber; Miocene (see Iturralde-Vinent & MacPhee [1996]).

Remarks.—This specimen conforms with the diagnostic characters of the genus given by Ramírez & Grismado (1997). Ramírez & Grismado (1997) performed a cladistic analysis of the filistatid genera, which are placed in two subfamilies, Filistatinae and Prithinae. Only males of the genera *Misionella* Ramírez & Grismado 1997 and *Pikelinia* Mello-Leitão 1946 have the metatarsus of the second leg modified, presumably to perform a clasping function during copulation. Extant species of both these genera are known only from South America and the Galapagos Islands (Grismado & Ramírez 2000; Ramírez & Grismado 1997; Müller 1987). These genera are distinguished from one another by the structure of the male palpal tibia. *Pikelinia* has a prominent dorsal retrolateral projection, whereas *Misionella* does not (Ramírez & Grismado 1997). The new fossil species differs from the two known extant species of *Misionella* in the structure of

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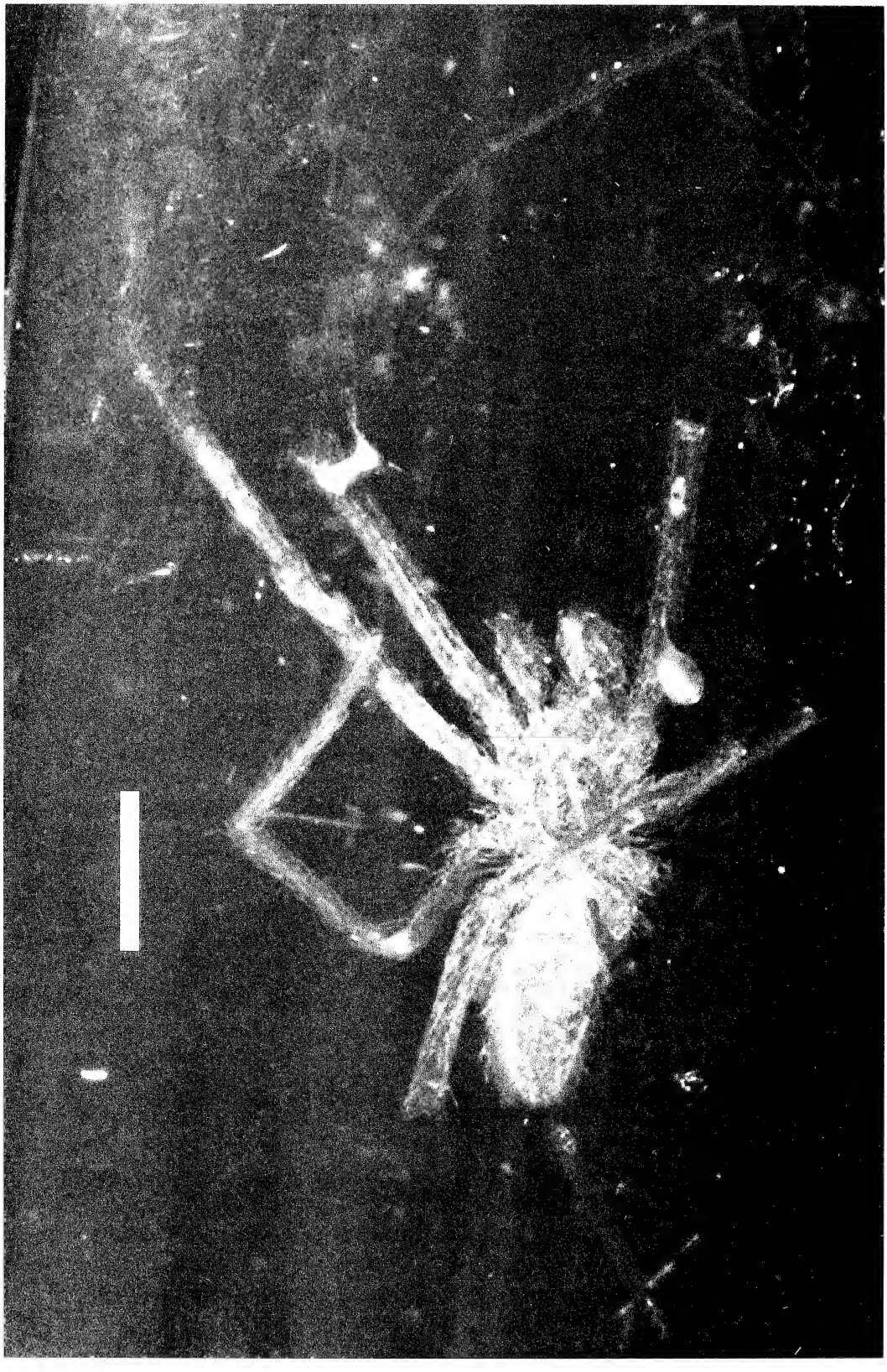
Figure 1.—Evolutionary tree of the Haplogynae. DRA = Dominican Republic amber (Wunderlich 1988; Penney 2001, this paper); SSC = Shanwang, Shandong, China (Dysderidae only; Zhang et al. 1994); MA = Mexican amber (Petrunkevitch 1971); B/BA = Baltic and Bitterfeld ambers (Menge 1854; Petrunkevitch 1950; Wunderlich 1981, 1991, 1993); AeP = Aix en Provence (Gourret 1888); NJA = New Jersey amber (Penney 2002a, 2004). Cladogram follows Coddington & Levi (1991); for details of evolutionary tree construction and terminology see Smith (1994). Not illustrated: Segestriidae described by Hickman (1957) and Oonopidae from Japan and Kenya (Nishikawa 1974 and Wunderlich 1981 respectively) may be extant species in Recent copal (e.g. Poinar 1992).



the pedipalp. In *M. mendensis* (Mello-Leitão 1920) the embolus is not spiralled but has only a slight kink and it does not extend beyond the paraembolic lamina; *M. jaminawa* Grismado & Ramírez 2000 has a hook-shaped embolus and lacks a paraembolic lamina. In addition, both extant species have small spinules in the retrolateral excavation of mt2; these are absent in the new fossil species. Based on the pedipalp morphology the new species is more closely related to *M. mendensis*.

DISCUSSION

The fossil and extant Hispaniolan spider faunas were reviewed by Penney & Pérez-Gelabert (2002). The only known filistatid from the island was the extant *Kukulcania hibernalis* (Hentz 1842), which is most certainly an introduced species (Penney 1999). Based on this observation, Penney (1999) hypothesized that Filistatidae may not have been present on Hispaniola during the Miocene when the amber was formed, and that the family had colonized the island more recently. The discovery of the new fossil falsifies this hypothesis and undiscovered extant species of *Misionella* may also exist on the island today. This new family record for the fossil fauna brings the number of families recorded from named species in Dominican Republic amber to 36 and the total number of families recorded to 45 (see Penney & Pérez-Gelabert 2002).

Misionella was formerly only recorded from extant species in Brazil and Argentina (Ramírez & Grismado 1997) although it probably has a wider distribution in South America. It is not included in species lists for Panama (Nentwig 1993), Costa Rica (Vega 1980), Cuba (Alayón-García 2000) and is not recorded from North America (Platnick 2003). Petrunkevitch (1928) considered the Greater Antillean spider fauna to represent an eastern outgrowth of the Central American fauna by way of a presumed earlier land connection and subsequent continent–island vicariance. However, such a land connection appears never to have existed (Ross & Scotese 1988; Iturralde-Vinent & MacPhee 1999). Iturralde-Vinent & MacPhee (1999) proposed that during the Eocene–Oligocene transition, the developing northern Greater Antilles and northwestern South America were briefly (33–35 Ma) connected by a landspan (a subaerial connection between a continent and one or more off-shelf islands) centered on the emergent Aves Ridge. This landspan consisted of a series of large, closely spaced islands or possibly a continuous peninsula stretching from northern South America to the Puerto Rico/Virgin Islands Block (Iturralde-Vinent & MacPhee 1999). The massive uplift that apparently permitted these connections was finished by 32 Ma (Iturralde-Vinent & MacPhee 1999). The Greater Antilles in their current guise are relatively young geographical features, probably no older than the middle Miocene. Therefore, all on-island lineages forming the Recent fauna must be younger than Middle Eocene (Iturralde-Vinent & MacPhee 1999). The known distribution of Recent and fossil species of *Misionella* supports the Greater Antillean–South America landspan hypothesis of Iturralde-Vinent & MacPhee (1999), rather than the Greater Antillean–Central American land connection hypothesis of Petrunkevitch (1928).

Roth & Roth (1984) defined autospasy as the separation of appendages, segments or parts thereof at a predetermined locus of weakness when the appendages or segments are restrained by any external (not self-induced) source. Entrapment in amber would constitute such a source. Autospasy occurs rarely in haplogynes but is known to occur in Filistatidae at the patellar–tibia joint. In the fossil, right legs 1 and 4 and left legs 1 and 3 have autospasized at this point and there are what I interpret as haemolymph exudations from the patella of right leg 1 and possibly also left leg 1 preserved in the amber (Figs. 2, 3), which indicates it had happened shortly after becoming entrapped in the resin. Indeed, the first pair of legs are preserved in the same piece of amber close to the spider, however they have rotated around approximately 180 degrees (Figs. 2, 3). This observation suggests

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Figure 2.—*Misionella didicostae* new species. Holotype male, Dominican Republic amber. Ventral view of whole specimen. Scale line 1.0 mm.

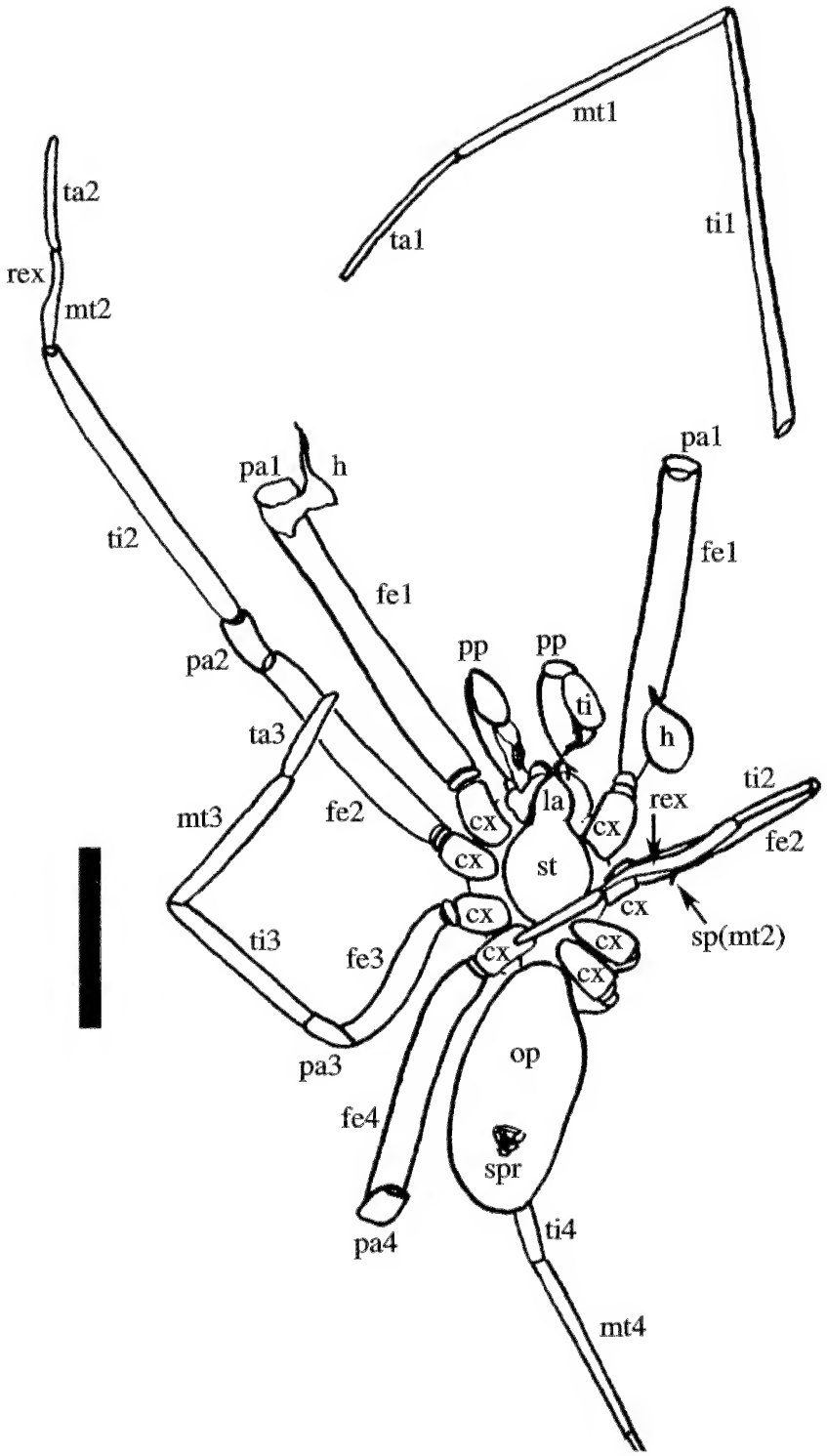
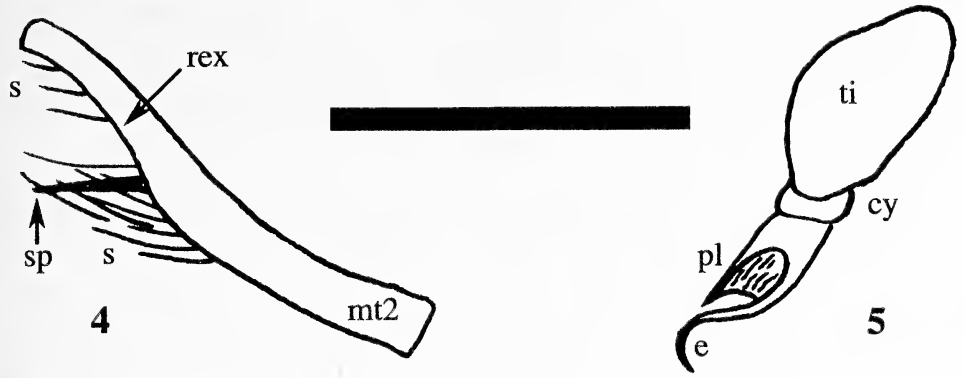


Figure 3.—*Misionella didicostae* new species. Holotype male, Dominican Republic amber. Camera lucida drawing of whole specimen. Scale line 1.0 mm. Refer to text for abbreviations.



Figures 4–5.—*Misionella didicostae* new species. Holotype male, Dominican Republic amber. 4, metatarsus 2. 5, pedipalp. Scale line 0.5 mm. Refer to text for abbreviations.

that the spider was engulfed in a flowing resin seep of relatively low viscosity, rather than having wandered onto a sticky exudate, becoming stuck and then covered by a subsequent resin flow, as is known to have occured in many cases of invertebrate amber preservation (Penney 2002b). Although Recent species of *Misionella* are primarily synanthropic, some have been collected from tree trunks (Ramírez & Grismado 1997). The discovery of this genus in amber is consistent with ecological observations of its Recent relatives.

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DIVERSITY AMONG GROUND-DWELLING SPIDER ASSEMBLAGES: HABITAT GENERALISTS AND SPECIALISTS

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ABSTRACT. We sampled assemblages of ground-dwelling spiders with pitfall traps in six terrestrial habitats representing a successional gradient in southwestern Virginia, during the summer of 2002. Approximately half of the 50 species trapped were habitat specialists with low abundance, found at only one of the sites, which is qualitatively consistent with the literature. Only four species, *Schizocosa ocreata* (Hentz 1844), *Pirata insularis* (Emerton 1885) *Pirata aspirans* (Chamberlain 1904) and *Neoantistea magna* (Keyserling 1887) were found at as many as four sites. A few species that were found in more than one study from disparate geographical communities, such as *Trochosa terricola* (Thorell 1856) tended also to be relatively abundant habitat generalists. In general, the majority of spider species found in studies such as ours that examined multiple sites were habitat specialists and had low abundance. For our sample sites, there was no relationship between any measure of spider diversity (*S, H', J'*) and successional age. Our results, and those of most other published studies, are consistent with the hypothesis that spider assemblages do not undergo succession and except for a few very common generalist species the composition of these communities is unpredictable, and may depend more on stochastic colonization and specific resource requirements of specialists following immigration than on any predictable association with successional parameters.

Keywords: Cursorial spiders, habitat specialization, spider diversity, succession

The importance of predators in the structure and function of natural ecosystems is becoming increasingly well documented (Terborgh et al. 2001). Spiders are widespread and diverse predators that are part of terrestrial arthropod assemblages (Wise 1993) and arthropods comprise more than half of known species (Wilson 1992). Cursorial spiders in particular are the dominant arthropod predators in many terrestrial communities, e.g., grasslands (Weeks & Holtzer 2000) and forest floor litter (Uetz 1979). Their position in trophic structure of communities often is complex: spiders in forest litter belong to both the decomposition and the grazing food webs because they consume detritivores/fungivores and herbivores (Uetz 1975; Wise et al. 1999). As larger species of wolf spiders mature, they prey more on herbivores that are part of the grazing food web (Uetz 1975; McNabb et al. 2001). Spiders have been experimentally demonstrated to exert important effects on the populations of other arthropods in a variety of experimental systems, including agricultural, old field, and forest litter communities (Hurd & Eisenberg 1990; Riechert & Bishop 1990; Moran et al. 1996; Lawrence & Wise 2000).

Given their demonstrated importance to the structure and function of many communities, it is important to gather information on the distribution and abundance of cursorial spider species. Often it has been difficult to determine what features of an environment determine which, or how many, species of cursorial spiders will be present. For example, spider diversity may not follow a trend toward increasing diversity with increasing successional age (Hurd & Fagan 1992; Aitchison & Sutherland 2000; Buddle et al. 2000) that has been a traditional expectation for species of plants and animals during terrestrial succession (Odum 1969).

Spiders have legendary powers of dispersal and often are among the first colonizers of disturbed sites (Hodkinson et al. 2001); the first known colonist of Krakatoa was a spider (Spiller et al. 1998). Many spiders have the ability to disperse by "ballooning" with silk at some point in their life cycles (Hodkinson et al. 2001). Lycosids and gnaphosids balloon

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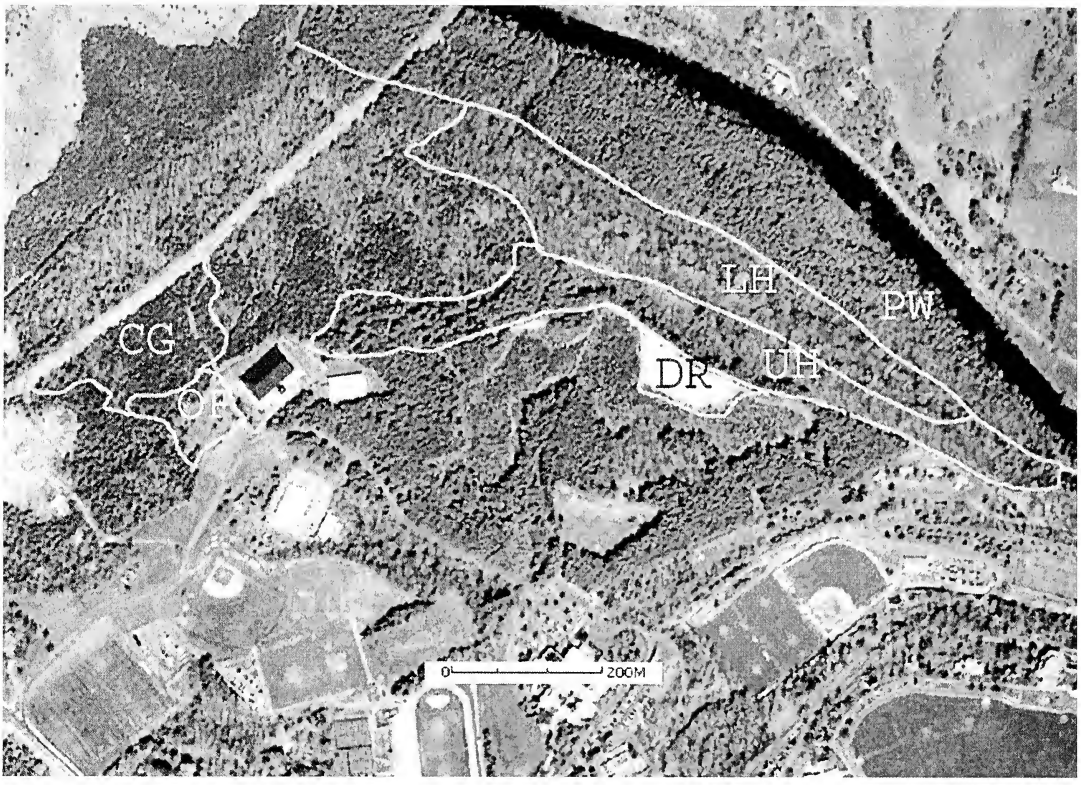

Figure 1.—Map of the Science Park on the campus of Washington & Lee University. The habitats used for sampling sites are described in the text: CG = cedar grove; OF = old field; DR = disturbance recovery; LH = lowland hardwoods; UH = upland hardwoods; PW = Pine woods.

as juveniles, while many linyphiids retain the capability throughout adulthood (Mrzljak & Wiegleb 2000). However adept they are at initially getting to new sites, cursorial spiders should have specific habitat preferences that dictate which species will become established and how abundant they will be. Some species are more particular than others: along a successional gradient in Delaware, the lycosid *Pirata insularis* (Emerton 1885) was found abundantly in all four communities examined, whereas the gnaphosid *Zelotes hentzi* (Barrows 1945) was rare and confined to the youngest successional site (Hurd & Fagan 1992). The structure of vegetation and some physicochemical habitat parameters may determine a spider's habitat choice (Mrzljak & Wiegleb 2000). Along forest litter gradients and in agroecosystems, lycosids manifest microhabitat preferences possibly based upon leaf litter, herbaceous vegetation and available moisture (Weeks & Holtzer 2000). The question of what determines the structure of cursorial spider guilds is far from being answered, and will require the accumulation of much more data (Uetz et al. 1999).

We report here on a field study in which six field sites, representing different successional seres, are compared with respect to ground-dwelling spider species captured by pitfall trap sampling. We compared diversity among sites, and the extent of habitat specialization (relative number of habitats in which species were found in this, and in previous studies) in these spiders.

METHODS

Study Sites.—The study sites we used for this study are located in the 35ha Science Park of Washington & Lee University in Rockbridge Co, Virginia, USA (Fig. 1). The sites were chosen to represent different habitat types and stages of secondary terrestrial succession typical of this region, as described below in order of successional age.

1. Disturbance recovery (DR): This site is

a 0.5ha patch of level ground, surrounded by woods, that is being used in a long-term study of community succession. The ground had been stripped of all native top soil prior to 2001, leaving a bare, hard clay surface. During fall and winter 2001 ground leaf mulch was applied to the bare clay and tilled into the upper 2–3cm, after which seeds of 19 native forb species and five native grasses were planted. The plant assemblage that sprouted during spring and summer 2002 constituted a dense mixture of these intentionally planted species and incidental species that were present as seed in the mulch (an especially conspicuous member of the second category during late summer was ragweed, *Ambrosia artemisiifolia*). The vegetation, which reached a height of approximately 0.5m, was dense enough to provide shade at the soil surface. There was no organic litter layer on the soil, owing to the absence of plants on the site during the previous year. This site is surrounded by a wire fence to keep out deer, and is surrounded by woods.

2. Old-field (OF): This site is a third year successional sere, which was previously subjected to mowing once or twice annually. It is fully open to the sun, and consists of grasses and forbs growing up to approximately 0.5m high typical of early successional old-fields in this region, including patches of emergent (ca 1.5m high) late-season goldenrod (*Solidago* spp.), teasel (*Dipsacus sylvestris*), and ragweed (*Ambrosia artemisiifolia*). Plant height and soil shading at this site were similar to those at site *DR* (see above), but here there was a sparse and shallow (≤0.5cm depth) litter layer consisting of dead plant stalks and leaves from the previous year's growth. An abundant and diverse arthropod assemblage inhabits this site, the most conspicuous of which are several species of grasshoppers (Acrididae). The cedar grove site (*CG,* see below) forms the western border of the old-field site.

3. Cedar grove (CG): This site consists of a near monoculture of 6–8m high eastern red cedar (*Juniperus communis*) from 30–40 years old, with a sparse understory of hardwood saplings and very little herbaceous ground cover. In our geographical area, cedars grow in old-fields until they shade out herbaceous vegetation, and then may dominate the community until they senesce and are replaced by hardwoods. The ground is mostly in shade, with small patches of sunlight most of the day. The soil is sandy and well-drained. The litter layer consists of a ≤ 1.0cm layer of dead cedar needles. We considered this site to be the earliest forest community, between *OF* and *PW* in age.

4. Pine woods (PW): This site is in deep shade, provided by an overstory of tall (≥10m) white pines (*Pinus strobus*) and mixed species of smaller hardwoods, especially red maple (*Acer rubrum*) and white ash (*Fraxinus americana*), with an understory of saplings and shrubs. This species mix represents an alternative intermediate stage of succession to the assemblage in *CG*; the relative height of the hardwoods in this stand indicated that *PW* may be the older of the two, at least 40 years old. The site is located on a flood plain, with relatively most soil. The litter layer is mainly dead needles, but somewhat thicker (≥1cm).

5. Upland hardwoods (UH): This site is within the woodlot boundary of the *DR* site. The overstory is of mixed hardwoods 10–15m high, especially white ash and tulip poplar (*Liriodendron tulipifera*), with several species of oaks (*Quercus* spp.), and red maple in the understory. This species mix is typical of the community that replaces coniferous species, i.e., perhaps 10–15 years older than site *PW* (i.e., 50–55 years old). The soil here is well-drained and rich in organic matter, with a relatively deep (3–4cm) leaf litter layer.

6. Lowland hardwoods (LH): This is a mature hardwood forest that has been subjected to little disturbance for at least the past 70 years, with canopy trees (tulip, maple, white ash, and mixed oak) ≥ 30m. This site is deeply shaded and is on a floodplain at the bottom of a slope, downward from site *UH.* The leaf litter is more compacted than and not as thick as at site *UH,* probably because of the increased soil moisture and humidity.

Sampling.—We sampled ground-dwelling spiders at each site with six pitfall traps set out in a 2 × 3 array, such that no trap was closer than approximately 1.5m from its nearest neighbor. Trap arrays were at least 10m from the edge of the habitats they sampled. Each trap consisted of a 10cm diameter, 11cm deep polypropylene cup fitted into a permanent sleeve that was sunk into the ground flush with the soil surface. A cover for each

Table 1.—Total numbers of cursorial spiders by habitat type (sampling site): DR = disturbance recovery; OF = old field; CG = cedar grove; PW = pine woods; UH = upland hardwoods; LH = lowland hardwoods. Superscripts denote other studies in which species were found: 1 = Hurd & Fagan (1992); 2 = Buddle et al. (2000); 3 = Aitcheson & Sutherland (2000); 4 = Bonte et al. (2002); 5 = Gajdos & Toft (2000); 6 = Uetz (1975); 7 = Uetz (1976); 8 = Uetz (1977); 9 = Uetz (1979); 10 = Buddle and Rypstra (2003); and 11 = Draney (1997). Nomenclature follows Platnick (2003).

Family	Genus;species	DR Total	OF Total	CG Total	PW Total	UH Total	LH Total	Species Total
Agelenidae Koch 1837	*Agelenopsis pennsylvanica*[1] Koch 1843						3	3
Antrodiaetidae Gertsch 1940	*Antrodiaetus unicolor* Hentz 1842			1	1			2
Corinnidae Karsch 1880	*Castianeira cingulata*[1, 6, 8, 9, 11] Koch 1841					1		1
	Castianeira longipalpus[1, 6, 7, 8, 9, 11] Hentz 1847					1	3	4
	Phrurotimpus alarius[1, 6, 8, 9] Hentz 1847			2		4	16	22
	Phrurotimpus borealis[3, 6, 9] Emerton 1911					3	2	5
	Phrurotimpus minutus[1, 6] Banks 1892					1	1	2
	Phrurotimpus sp. Chamberlin & Ivie 1935					1	1	2
	Scotinella britcheri Petrunkevitch 1910		1					1
	Scotinella formica[1] Banks 1911	1	8					9
	Scotinella sp. Banks 1911						1	1
Cybaeidae Banks 1892	*Cybaeus sp.* Koch 1868				3	1	1	5
Dysderidae Koch 1837	*Dysdera crocata*[4] Koch 1838		1					1
Gnaphosidae Pocock 1898	*Drassyllus depressus* Emerton 1890		1					1
Hahniidae Bertkau 1878	*Hahnia cinerea*[3, 9] Emerton 1890			1		5		6
	Antistea brunnea Emerton 1909				1	1		2
	Hahnidae *sp. 1*					1	3	4
	Neoantistea agilis[3, 11] Keyserling 1887		1	1				2
	Neoantistea magna Keyserling 1887		1	1	1	1		4
Linyphiidae Blackwall 1859	*Drapetisca alteranda* Chamberlin 1909				1			1
Subfamily: Linyphiinae	*Stemonyphantes lineatus* Linnaeus 1758		1					1
	Tenuiphantes zebra Emerton 1882					1		1
Lycosidae Sundevall 1833	*Allocosa funerea*[1, 11] Hentz 1844	2	1					3
	Allopecosa aculeata Clerck 1757	1						1
	Arctosa virgo Chamberlin 1925			1				1
	Hogna helluo[1, 6, 10] Walckenaer 1837		1	1				2
	Pardosa distincta[1] Blackwall 1846	2	1					3
	Pardosa milvina[1, 10, 11] Hentz 1844	11						11
	Pardosa saxatilis[1, 6] Hentz 1844	16						16
	Pardosa sp. 1 Koch 1847				1			1
	Pardosa sp. 2 Koch 1847	7						7
	Pirata aspirans[1, 6] Chamberlin 1904	1	2		1		2	6

Table 1.—Continued.

Family	Genus;species	DR Total	OF Total	CG Total	PW Total	UH Total	LH Total	Species Total
	Pirata insularis[1, 3, 6] Emerton 1885			25	37	1	141	204
	Rabidosa rabida[1, 11] Walckanaer 1837		5					5
	Schizocosa avida[1] Walckanaer 1837	3	4					7
Lycosidae Sundevall 1833	*Schizocosa bilineata*[1, 11] Emerton 1885		2					2
	Schizocosa ocreata[1, 6, 7, 8, 11] Hentz 1844			6	1	5	3	15
	Trochosa terricola[1, 2, 3, 4, 5] Thorell 1856	2	1					3
	Trochosa sp Kock 1847					1		1
Oonopidae Simon 1890	*Orchestina saltitans* Banks 1894	1						1
Oxyopidae Thorell 1870	*Oxyopes salticus*[1, 11] Hentz 1845		2					2
Philodromidae Thorell 1870	*Thanatus formicinus*[11] Clerck 1757		1					1
Pisauridae Simon 1890	*Dolomedes tenebrosus* Hentz 1844	1					1	2
Salticidae Blackwall 1841	*Habronattus borealis* Banks 1895	1						1
	Neon nelii[3] Peckham & Peckham 1888	1				1		2
Theridiidae Sundevall 1833	*Euryopsis argentea* Emerton 1882					1		1
Thomisidae Sundevall 1833	*Ozyptila sp.* Simon 1864		1					1
	Xysticus ferox[1, 7, 9, 11] Hentz 1847			1		1		2
	Xysticus punctatus Keyserling 1880							0
	Xysticus sp. Koch 1835			1				1
Habitat Total Abundance =		50	35	41	47	31	178	382

trap was constructed using a Petri dish lid with nails to elevate it 3cm above the lip of the trap. These covers kept out rainwater and falling debris. Sampling occurred at weekly intervals from early June to mid-August, and then once at the end of September 2002 (total = 354 trap-days). Each time we sampled, we put approximately 2cm of 70% ethanol into each trap during the afternoon (ca 1600h), and collected the samples 16–18h later.

All adult spiders collected from the traps were counted and identified using taxonomic keys (Kaston 1978, 1981; online taxonomic updates http://kaston.transy.edu/spiderlist/Kaston78.htm and http://kaston.transy.edu/spiderlist/kast.htm; Roth 1993). Our nomenclature follows Platnick (2003). We did not attempt to enumerate or identify to species spiders in the subfamily Erigoninae (family Linyphiidae), which were infrequently captured, and most of which were represented by a single individual. At least one individual of each species collected (a male and female of each, when available) was preserved in Kahle's fluid as part of a reference collection.

As with any field study in a diverse species assemblage, sampling efficacy is not likely to be equal among taxa. In the case of pitfall traps, for instance, the most active spiders (e.g., many lycosids) may have a tendency to be disproportionately sampled relative to more sedentary species (e.g., clubionids). Therefore, species richness and relative abundance of captured spiders may not accurately reflect the entire resident assemblage, but can be used for comparisons among sites of those taxa that are susceptible to pitfall trapping.

Data analysis.—We compared sampling

Table 2.—The number of shared cursorial species between habitats, and species diversity (richness = S; J′ = evenness; Shannon's diversity = H′) for each habitat based on pit trap samples. Sites arranged in order of increasing successional age from left to right and top to bottom. Site descriptions given in Methods.

Sites:	DR	OF	CG	PW	UH	LH
DR	**14**	—	—	—	—	—
OF	6	**18**	—	—	—	—
CG	0	3	**12**	—	—	—
PW	1	2	4	**9**	—	—
UH	1	1	6	5	**18**	—
LH	2	1	3	4	9	**13**
H′ =	*2.06*	*2.57*	*1.45*	*0.94*	*2.63*	*0.96*
S =	*14*	*18*	*12*	*9*	*18*	*13*
J′ =	*0.78*	*0.89*	*0.58*	*0.43*	*0.91*	*0.37*

sites with regard to diversity, measured as (1) the number of species found, or species richness, *S,* (2) Evenness of distribution of individuals among species, *J'*, and (3) Shannon's diversity, *H'*, which is a measure of the interaction between evenness and richness (Pielou 1969; Hill 1973).

RESULTS

We collected a total of 50 species of ground-dwelling spiders from our six sampling sites (Table 1). Twenty-six of these were habitat specialists, found at only one site; no species was found at all six sites. The spiders with the broadest distribution, found at four of the six sites, were the lycosids *Schizocosa ocreata*, *Pirata insularis*, *Pirata arenicola* and the hahniid *Neoantistea magna*. Both *S. ocreata* and *P. insularis* were found at all four wooded sites and none was collected at either of the open field sites. However, *P. arenicola* and *N. magna* were found at combinations of wooded and open field sites.

Some of the spiders we found appear to have wide geographical distributions. Five species in Table 1 were also reported in four or more other studies from Denmark, Belgium and Manitoba, as well as sites in the U. S. (Delaware, Ohio, Georgia and Virginia). However, there appears to be no reliable relationship between how broadly cursorial spider species are distributed among geographic sites, how many sites they occupy within a study, or what kind of habitat (e.g., wooded or open) they prefer in those studies that sampled more than one habitat type.

We found no relationship between successional age and any measure of diversity (Table 2). The pine stand (PW), representing the intermediate stage of succession, had the lowest spider diversity (Table 2). This site also had the lowest apparent vegetational diversity among the six sites: there was almost no ground cover vegetation, and the tree diversity was limited to white pine and a few small deciduous saplings. However, there were no other apparent correlative trends between spider diversity and site structure. The highest *H'* diversity and *J'* evenness values we found were in the nearly mature forest (UH), and the old field (OF), our second to youngest site, yielding virtually identical rank abundance patterns (Fig. 2). Although species richness was the same (18) for both of these sites, they only shared a single species, *N. magna* (Table 2). The climax forest (LH) had the lowest *H'* value even though species richness was about average among the sites. This was because of the high dominance of a single species (*Pirata insularis*), which was reflected by the low value of *J'* (Tables 1 & 2).

Our most abundant species trapped was *P. insularis*, accounting for more than half of all spiders trapped (Table 1). The abundance of *P. insularis* in our traps was highest in mid-June, decreasing to just two individuals caught in August and September. From the beginning of the sample season, the sex ratio of this species was highly male-biased. As the season progressed it shifted to a female-biased ratio. July appeared to be the month of reproduction: females were caught with egg sacs on 2 July, and with juveniles riding on the dorsa of their abdomens on 10 and 19 July.

We also were able to record some repro-

ductive data for *S. ocreata* and *P. saxatilis*. On 1 July we found a female *S. ocreata* with a new (white) egg case. On 10 July a female with a gray (older) egg case was captured. The case was dissected and almost fully developed eggs were found inside, with fangs evident. On 19 July a female was caught with juveniles on her back. On 20 June we found a female *P. saxatilis*, with an egg case. On two other occasions (2 and 17 July) we found females with egg cases. On 26 July we found one with spiderlings on her dorsum, and brought it back to the lab for observation. On 29 July spiderlings were seen leaving the mother's dorsum and by 30 July they had all dispersed.

DISCUSSION

As with previously reported studies, we found that most ground-dwelling spider species were habitat specialists, found at one or two sites, and very few were generalists. Because rare species may be present in such low numbers that they may be missed by sampling, we cannot conclude that a species that did not show up in our samples was completely absent from a given site, but we can at least score a species as present if we captured it in a sample. This is a problem common among studies that report the presence of rare species, many of which are represented by a single trapped individual (e.g., 31 of 105 species reported by Buddle et al. 2000).

Both Aitchison & Sutherland (2000) and Hurd & Fagan (1992) found only three species that occupied four or more sites; we found only four species in that category. However, very few of these are the same species. Six of the species we found were also reported from these two studies in Manitoba, one of which (*Trochosa terricola*) was found in both Manitoba studies and in our present study (Table 1) and has been reported to occur from as far away as Finland (Aitchison & Sutherland 2000) and Belgium (Bonte et al. 2002). Not surprisingly, there were more spider species (20) in common between our present study and the geographically closer Delaware sites of Hurd & Fagan (1992). The most abundant species in both the present Virginia study and the Delaware study was the lycosid, *Pirata insularis*.

The majority of spiders we encountered belonged to the family Lycosidae. While *P. insularis* preferred wooded sites, the next two most abundant lycosids (*Pardosa milvina* and *P. saxatilis*) were confined to the most open site (DR). Buddle & Rypstra (2003) also noted that *Pardosa* species achieve dense populations in barren exposed habitats. *Schizocosa ocreata* was found in all four wooded sites. This species is commonly found in leaf litter of deciduous forests in eastern North America (Wagner & Wise 1996). Uetz (1977) noted that *S. ocreata* occurs in simple litter where the leaves are compressed and the ground is relatively moist.

The diversity of sampled spiders in our study did not follow a successional gradient, a finding of other studies as well: a forest successional gradient in Delaware (Hurd & Fagan 1992), and forests in Manitoba (Aitchison & Sutherland 2000; Buddle et al. 2000). Part of the difficulty may lie in the relative scarcity of studies that examine a wide range of successional seres at a given locale. In any event, attempting to find predictable environmental correlates to spider diversity have proved frustrating for many researchers. In their 20 year study of coastal dunes Gajdos & Toft (2000) found that temporal changes in community composition were greater than differences occurring between habitats. It was impossible for them to determine what ways ecological characteristics changed for those spider species in which abundance changed over time. Differences in the physical structure of leaf litter and its complexity can influence species composition, spider abundance and diversity generally increasing with increased litter depth in some studies (Uetz 1975, 1977, 1979; Buddle & Rypstra 2003). Uetz (1975) found that weather patterns, which could be tied to prey productivity for spiders, did not correlate significantly to any diversity measure. Instead, he found that richness and evenness were related to litter depth, and moderately well related to successional age and plant cover. However, in our study we found as many spider species in the two open habitats with almost no litter (DR and OF) as we did in the two hardwood forest habitats (UH and LH). Mrzljak & Wiegleb (2000) presented evidence that species richness and abundance are limited by vegetative stratification and height, e.g., tall grass stands had more species than short grass stands. Hurd & Fagan's (1992) study of spider assemblages in Delaware found the main difference to be between

woodland and open habitats and not age of the habitats: diversity of cursorial spiders generally was greater in open field habitats than in woodlands. However, in our present study we found no clear difference among sites based on presence, absence, or extent of tree cover.

It is apparently not difficult to predict the presence in spider assemblages of some very broad generalists such as *Trochosa terricola*, but for most habitat specialists, such prediction is problematic. Given the data so far, it is hard to refute the null hypothesis that spider diversity within a site may be more a function of stochastic colonization opportunities of different species rather than a set of intra-community assembly rules (*sensu* Diamond 1975). Other factors that can influence species membership in arthropod assemblages, including spiders, are habitat features such as area, degree of isolation, and movement patterns of animals relative to their resource requirements (Matter 1996, 2000; Hanski 1999; Marshall et al. 2000; Samu et al. 2003). Thus, changing spider community composition over time is not really true succession at all, but rather repeated colonization by opportunistic species. The success of such colonists, once they invade a habitat, may well depend on competitive abilities (Marshall et al. 2000) and the changing environmental conditions that accompany plant succession (Mrzljak & Wiegleb 2000; Hodkinson et al. 2001), but as yet we are far from being able to predict cursorial spider composition among seres with any degree of precision.

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SEASONAL HABITAT SHIFT IN AN INTERTIDAL WOLF SPIDER: PROXIMAL CUES ASSOCIATED WITH MIGRATION AND SUBSTRATE PREFERENCE

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ABSTRACT. During most of the year, the wolf spider *Pardosa lapidicina* Emerton 1885 occupies tidal cobble beaches surrounding Narragansett Bay, RI, USA, but in late autumn part of the population moves into adjacent forest litter to overwinter. We monitored these movements with drift fences and pitfall traps from 1996–1999 and evaluated the possible roles of ambient temperature, rainfall, humidity and storm events. We tested substrate choice over the season as a proxy for migratory tendency, both in the laboratory and the field, focusing on the roles of temperature and photoperiod. The timing of peak migration differed among years (S.D. = 15.5 d). Minimum weekly temperature, weekly rainfall, percent relative humidity and storm events did not explain the variation in migratory times. However, significantly more spiders migrated during weeks with below-freezing temperatures than in weeks without them. Leaf litter, which has less variable temperatures than beach cobble, may provide a refuge from extreme temperatures during winter. Spiders maintained at cold temperatures in laboratory experiments chose leaves over beach cobble significantly more often than did those in warm temperatures. The time of year that spiders were collected also influenced their probability of choosing leaf substrate in the laboratory. Photoperiod, on the other hand, did not significantly influence substrate preference. This study helps to uncover how environmental cues influence seasonal movements across a habitat boundary.

Keywords: Acclimation period, photoperiod, substrate, temperature

Migration is a common behavioral response to seasonal change in temperate-zone organisms, providing them with the opportunity to exploit otherwise unavailable seasonal resources or escape temporarily inclement conditions (Tauber et al. 1986; Dingle 1996). The timing of these movements, often from one habitat type to another, is essential to the survival and reproduction of the migrant. Thus, seasonal migration likely requires both the use of environmental cues to indicate optimal timing of movement and major shifts in behavior, such as substrate choice preference. Two environmental variables, temperature and photoperiod, frequently indicate the oncoming habitat deterioration for temperate-zone terrestrial species and play a major part in their seasonal movements (Schaeffer 1977; Delisle and McNeil 1987; Han and Gatehouse 1991; Tanaka 1997). These cues help migrants to anticipate or respond directly to seasonally deleterious aspects of their environment, such as low temperatures and freezing conditions, by triggering physiological and behavioral changes (Tauber et al. 1986).

Although long-distance movements like those of some birds and butterflies capture much of the attention surrounding migration, considerably shorter movements by less mobile animals are likely a frequently occurring phenomena. Despite the short distance, these migrants may cross abrupt physical boundaries, including such markedly dissimilar habitats as marine or freshwater-influenced to terrestrial locales (Svensson & Janzon 1984; Takada 1995; Madsen & Shine 1996), epilithic to benthic habitats (Kornijow 1992) and elevational gradients (Kimura & Beppu 1993). Crossing the boundaries exposes migrants to novel substrate. To survive in a drastically different environment, the migrants are often forced to make behavioral changes, potentially including a changed preference for sub-

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strate in the 'new' environment. Whether this change in preference occurs, and how it may be related to actual migratory tendency, has not, to our knowledge, yet been tested.

We studied the effect of photoperiod, temperature, humidity and storm events on the timing of migration by the intertidal wolf spider *Pardosa lapidicina* across a marine intertidal-terrestrial boundary. We further asked how substrate choice is associated with seasonal movement in the field, and how important seasonal cues such as temperature and photoperiod influence substrate preference. Populations of *P. lapidicina* in Bristol County, RI, USA, spend all but the winter months on cobble beaches immediately above the tide line, but in November and December some individuals retreat from the beach to the adjacent forest where they overwinter. Though not a lengthy move (5–15 m, Morse 1997), it spans two totally different adjacent ecosystems (see Polis & Hurd 1996). The spiders are exposed to substrates of strikingly contrasting texture and conductance (stones and pebbles vs. leaves): one familiar, one novel. Although short-distance movements (<1 m) from vegetation to ground hibernacula are common in spiders, larger seasonal movements of several meters are rare (Schaeffer 1977).

Winters in the study area vary markedly in their severity (Morse 1997). For example, snow and ice covered the beach from January through mid-March in 1994, making it uninhabitable for spiders during that time, whereas the 1995 winter was snowless, allowing a small number of spiders to persist on the upper beach throughout the winter (Morse 1997). We hypothesized that as a result this beachside species should respond variably to changing seasons (Hopper 1999; Tammaru et al. 1999; Comeau et al. 2002). During cold winters, temperature extremes, storm events and freezing weather the rocky shore may become extremely deleterious to the spiders (Morse 1997). Under these conditions, *P. lapidicina* should benefit from anticipating the onset of winter and leaving the beach. During mild winters, the spiders may benefit from delaying migration temporarily or indefinitely and feeding on the beach.

We hypothesized that spiders would use photoperiod as an indicator of the onset of winter, but might only respond with movement if temperatures reached some minimal threshold. Furthermore, we expected that large winter storm events would force spiders to leave the beach. Humidity has been shown to influence seasonal movements in another species of wolf spider (Eubanks & Miller 1993), probably due to their high susceptibility to desiccation. Although very dry conditions are unlikely at our study sites because fresh water drains from upslope towards the shore, we expected that humidity could play a role in the seasonal movement of these spiders. In terms of substrate choice, we hypothesized that substrate preference would be closely related to predilection to migrate, since migration required moving to a novel substrate. We therefore predicted that the cues affecting substrate preference would mirror those cues influencing migration in the field and that substrate could be used to examine those patterns experimentally. Preliminary evidence suggested that cold temperatures increase the preference of wolf spiders for leaf substrate (J.M. Kraus, unpubl. data).

To test these hypotheses, we used a combination of field observations and experiments in the laboratory and field. We monitored the movements of these spiders from cobble beach to forest leaf litter using drift fences and pitfall traps during the autumn over four fall seasons (1996–1999). We then examined the relationship between migration and common seasonal cues or deleterious events that might affect the spiders on the beach (temperature, photoperiod, moisture, storms). To investigate the relationship between migration and substrate preference, we ran substrate choice experiments in the field and compared the results with migration patterns. We tested for the influence of photoperiod and temperature on substrate preference in the laboratory to establish the role of these common migratory cues on substrate preference. We used temperature probes to measure the thermal conditions in cobble and leaves before, during and after migration, since consistently warmer temperatures might convey benefits for migrating into the leaf litter in winter.

METHODS

Study subjects.—*Pardosa lapidicina* in Bristol County, RI, USA have a one-year life cycle. During the reproductive seasons of spring and summer, the spiders regularly follow the receding tide into the intertidal area

where they prey primarily upon small Diptera and Collembola (Morse 1997). Spiders disappear from the low intertidal in mid-October. Density on the high intertidal and supratidal decreases in late November and December as numbers caught in the forest leaf litter increase (Morse 1997). Spider density on the beach remains low from December–March, although a portion of the population overwinters on the upper beach. In March and April the density on the beach increases again, as the spiders migrate back to the beach, and then decreases a last time as that cohort dies after reproducing in June and July. These spiders were never found in the forest or forest-beach interface until the fall when they made their decision to overwinter in the forest or on the beach (Morse 1997). It appears that they do not contact the forest environment until the late fall, unless a storm event inundates the beach. Like other *Pardosa* species (Vogel 1971; Lowrie 1973; Fujii 1974), *P. lapidicina* are small, cursorial and nomadic. They are dark-colored and 6–9 mm in length, with the females somewhat larger than the males (Kaston 1948). By migration time in November, they weigh 15–45 mg (J.M. Kraus, unpubl. data). In the study area individuals overwinter as juveniles, usually in the penultimate or antepenultimate stages (Morse 1997). We have no evidence that they overwinter as adults. Morse (1997) estimated about 2000 spiders entered winter in 1993 along a cobble beach 120 m long (17 spiders/m transect). Voucher specimens of *P. lapidicina* have been deposited in the National Museum of Natural History, Smithsonian Institution.

Study area.—We studied the spiders at two sites on the Haffenreffer Estate of Brown University, Bristol Co., RI. The research area consists of a cobble beach and adjacent forest on the west shore of Mt. Hope Bay, a partially sheltered arm of Narragansett Bay. Most cobble rocks range from 10–30 cm in diameter, and larger stones and bedrock protrude in some places (Morse 1997). The cobble bed is several rocks deep. The forest consists predominately of hackberry *Celtis occidentalis*, red oak *Quercus rubra* and red cedar *Juniperus virginiana* under 20 m, with bittersweet *Celastrus orbiculatus*, greenbrier *Smilax* sp., and poison ivy *Rhus radicans* often climbing into the canopy. Other than the vines, ground cover is sparse, but a heavy layer of leaf litter persists throughout the year (Morse 1997). Ambient temperatures on the beach within 1–2 m of the forest may drop from over 20 °C in early November to −17 °C by late December. Study sites were separated by over 100 m, and by boulders and vegetation (see Morse 1997 for details).

Seasonal movement.—To monitor spider movement from beach to forest, 15 m drift fences were used at two forest sites 5 m from the cobble beach/forest interface and parallel to it. The fences, ca. 0.5 m high, consisted of heavy clear plastic sheeting that was supported by rebars driven into the ground approximately 1 m apart. The bottom of the plastic sheeting was buried under several cm of soil. *Pardosa lapidicina* are non-burrowing wolf spiders and it is very improbable that they could have moved under the fences. Pitfall traps, 1 liter plastic containers of 12 cm diameter, were sunk flush with the ground at approximately 1 m intervals on the beach side of the fences to trap individuals moving directly away from the beach and on the forest side of the fences to measure lateral movement around the fences. Leaves and small stones were added to the bottoms of the traps to provide cover and to discourage cannibalism. The total number of spiders captured was used as an index of migration over that trap period. The weekly ratio of spiders captured on the forest side to total catch was used as a conservative estimate of nonmigratory spider activity in the forest.

Trapping began in late October, based upon preliminary data on the timing of seasonal movements (Morse 1997), which showed no capture of spiders by hand searching in the 5 m strip of forest above the beach and by using pitfall traps 3 m into the forest from early September until 14 November in 1993 (Morse 1997). Additionally, an intensive search of the forest from May–November 1994 (0.1–10 m above the beach) turned up no individuals until 6 November (Morse 1997). Drift fence traps were monitored weekly from late October or early November through mid to late December 1997–1999, and twice weekly in 1996. Spiders were brought to the laboratory, weighed, sexed and then released on the landward side of the fences. Rate of recapture in the fences was estimated in 1997 by marking spiders caught in the fences at the beginning

and end of November with orange micronite dye (Morse 1997) and noting their recapture.

Ambient temperature was recorded at the time of all censuses and field experiments. Daily minimum temperature, maximum and minimum relative humidity, weekly rainfall and storm events of the local region were obtained from recorded NOAA (National Oceanographic and Atmospheric Administration) weather station data at the T.F. Green Airport in Providence, RI, 17 km to the WNW (NOAA 1996–1999). All statistical analyses were performed using SAS statistical software (SAS Institute, Inc. 1989) unless otherwise noted. The relationship between temperature, rainfall and humidity measurements taken between trapping periods and spider movement at the end of that period was examined using NOAA data to investigate the potential influence of these factors on migration during 1996–1999. The effect of storm events and days below freezing were independently evaluated using Wilcoxon non-parametric statistics to evaluate the one-way hypothesis that larger migrations would occur during weeks of storm events and freezing weather.

In 1999, one temperature probe from a HOBO H8 data logger (Onset Computer Corp., Bourne, MA, USA) was placed in each of four habitat types at a central site: ambient in shade 1 m off ground 5 m into the forest, ambient in open 1 m off ground at the beach-forest edge, under leaves 5 m into the forest, and under rocks on the upper part of the beach. The probes recorded ambient temperature every 10 min from early November to late December. Daily temperature variation (s^2) was compared among microhabitats using a 1-way ANOVA. Differences among means were then tested using the Ryan-Einot-Gabriel-Welsch multiple range test.

Substrate choice in the field.—Substrate choice experiments were performed weekly for 14 weeks in the field during 1997 using spiders hand-collected from the upper beach (20 per trial), and in 1997 and 1999 using those captured in pitfalls that week (7 test periods in 1997, 5 test periods in 1999). The substrate choice arenas were plastic tubs (32 cm × 18 cm × 10 cm), one half lined with beach cobble and the other half with forest leaf litter. Fresh substrate was used for each run. Spiders already in the leaf litter were extremely difficult to locate by hand (Morse 1997), and as a result only spiders caught in forest pitfalls were used for the already-migrated spiders in the substrate choice experiments.

Substrate choice arenas were placed at the intersection of the cobble beach and forest leaf litter perpendicular to the tide line. The containers were alternated so that the cobble faced the forest in half of the arenas and the leaves faced the forest in the other half, thus controlling for the effect of orientation on spider movement. Spiders were placed in the containers at the interface of the leaves and the substrate, and their location was recorded after 3 h. Pilot studies indicated that the spiders explored the container actively for the first 1.5 h, after which their rate of movement greatly declined (D.H. Morse pers. obs.). The 3 h acclimation period was used as a conservative estimate of the time needed for the spiders to explore their habitat thoroughly and make a choice. If the spider escaped before the end of the experiment, it received a "no choice" rating and was removed from the analysis. We used logistic regression to examine whether substrate choice varied over time (both by year and month collected), migration status (1997) or substrate orientation.

Substrate choice in the laboratory.—In Fall 1999, we investigated the effects of temperature and photoperiod on substrate preference under controlled laboratory conditions using a 2 × 2 × 5 factorial design: two levels of temperature (cold/warm), two levels of day length (short/long) and five time periods (12–15 Sept., 5–7 Oct., 4–7 Nov., 21–23 Nov., 13–15 Dec.). Substrate choice was measured in the same arenas used in the field. Treatments were replicated 30 times for a total of 600 spiders. The collection dates were chosen to reflect dates before, during and after migration in the field.

Spiders were collected at each of the four collection dates from the beach and immediately acclimated for 8 d before the experiments were run in the experimental arenas. Treatment conditions were maintained in two environmental chambers, one cold (4—6 °C), one warm (22—28 °C). Within each chamber a lightproof partition separated short (9 h, 40 min) and long (12 h, 40 min) day-length conditions. One 20 watt earthlight bulb in each side of the chambers provided appropriate day length. Temperature and photoperiod were not

alternated among chambers over the duration of the experiment due to mechanical constraints. The cold/short treatment simulated temperature and light conditions in mid-November, when previous data indicated the peak migration occurred (Morse 1997). The warm/long treatment simulated conditions in mid-September. The cold/long and warm/short treatments served as controls to separate the independent effects of temperature and photoperiod on substrate choice. The statistical model included temperature, photoperiod, time, and all interactions and was evaluated using a generalized linear model to perform logistic regression on binomial data (PROC GENMOD). All factors were considered fixed because they were set a priori by the investigators to sample different populations.

On each collection date we obtained 120 spiders from the beach 50 m or more from the drift fences, and maintained them individually in 15 dram vials (6.0 cm long, 3.5 cm diameter) with a 3 cm × 3 cm moistened square of paper toweling. Thirty spiders were randomly assigned to each treatment immediately after collection and remained in the chambers for an 8 d acclimatization period. On the third and sixth days of this period, they were all fed one *Drosophila melanogaster*, and their toweling was moistened to maintain uniform humidity. Instances of feeding (whether the fly was consumed) and molting were recorded. We analyzed the main effects of the treatment and collection date on whether an individual molted or fed, using logistic regression (PROC GENMOD).

On the eighth day, experimental arenas were prepared in the same way as the field experiments and then placed in the environmental chambers for 1 h before the spiders were introduced to bring their materials into equilibrium with the air temperature. Spiders were placed, one per container, at the interface of the cobble and leaves (on a rock and under a leaf), and substrate choice was recorded after 3 h. If the spider did not move (which was extremely rare) or if it escaped before the end of the experiment, it received a "no choice" rating and was removed from the analysis. The spiders were released at their original field site during the following week.

All substrate choice trials for both field and laboratory were analyzed with a chi-square test for goodness of fit to examine whether the substrates were chosen in equal proportions. Data were summed over the whole season when sample sizes for a week's trial were not adequate for individual analysis (Sokal & Rohlf 1995).

RESULTS

Seasonal migration.—Yearly drift fence captures (1996–1999) totaled 59, 66, 38 and 28 individuals, respectively, peaking between early November and early December in different years (Fig. 1). Drift fence data were summed over both fences for all analyses due to low sample size. The difference in day length between the two extremes (2 Nov. 1997 and 6 Dec. 1998) was 64 min. The percentage of spiders captured on the side of the fences facing the beach changed over the years, but was consistently more than 2 times as large as the proportion captured behind the fences: 1999, 82% in front; 1998, 71% in front; 1997, 96% in front; 1996, unknown. Also, the overall rates of recapture behind the fences were low. Of the 33 spiders that were marked after being captured at the fences on 2 Nov. and 30 Nov. in 1997, only one was recaptured (3%) after being released behind the fence.

No significant relationship occurred between numbers that migrated and minimum ambient temperature in the week preceding a collection at the pitfall traps (correlation analysis, $R = -0.13$, $n = 44$, $P > 0.05$), but migration did occur significantly more frequently during periods containing episodes of freezing weather (Wilcoxon 2-sample one sided exact test, $n_{\text{above freezing}} = 15$, $n_{\text{freezing or below}} = 29$, $P = 0.047$; Fig. 2). Neither weekly rainfall (correlation analysis, $R = 0.13$, $n = 44$, $P > 0.05$), nor percent relative humidity (correlation analysis, available for 1996–1997 only; min $R = -0.17$, $n = 27$, $P = 0.41$; max $R = -0.24$, n = 27, $P > 0.05$) correlated significantly with migration, and migration did not occur more frequently during weeks with storm events than those without storms (Wilcoxon 2-sample one sided exact test, $n_{\text{storm}}=7$, $n_{no\ \text{storm}} = 39$, $P > 0.05$). Although the mean temperature was similar at all microhabitat sites, the variation (s^2) in daily temperature within fallen leaves was more than three times less than in the cobble, in the shade above the leaves, or in the sun above the leaves in 1999 (Table 1).

Substrate choice in the field.—A total of 280 spiders collected from the beach were

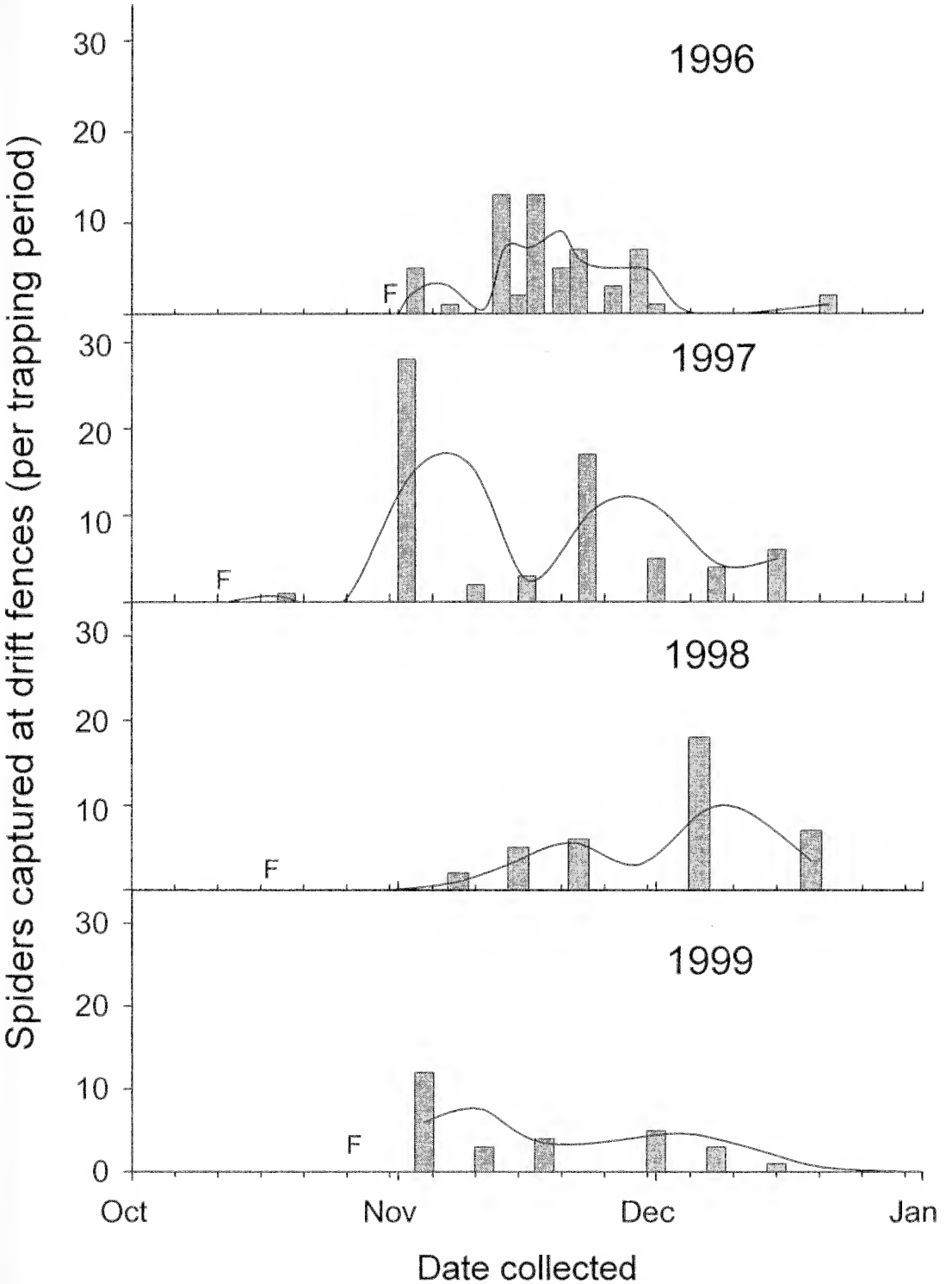

Figure 1.—Number of spiders captured at the two drift fences, 1996–1999. Sample sizes were too low to analyze each fence separately. Bars represent number captured during trapping period (ranging from several days to a week). Lines are running average number of spiders captured over two trapping periods. "F" indicates first date of trapping. Traps ran continuously throughout season. Initiation of trapping was dictated by preliminary data.

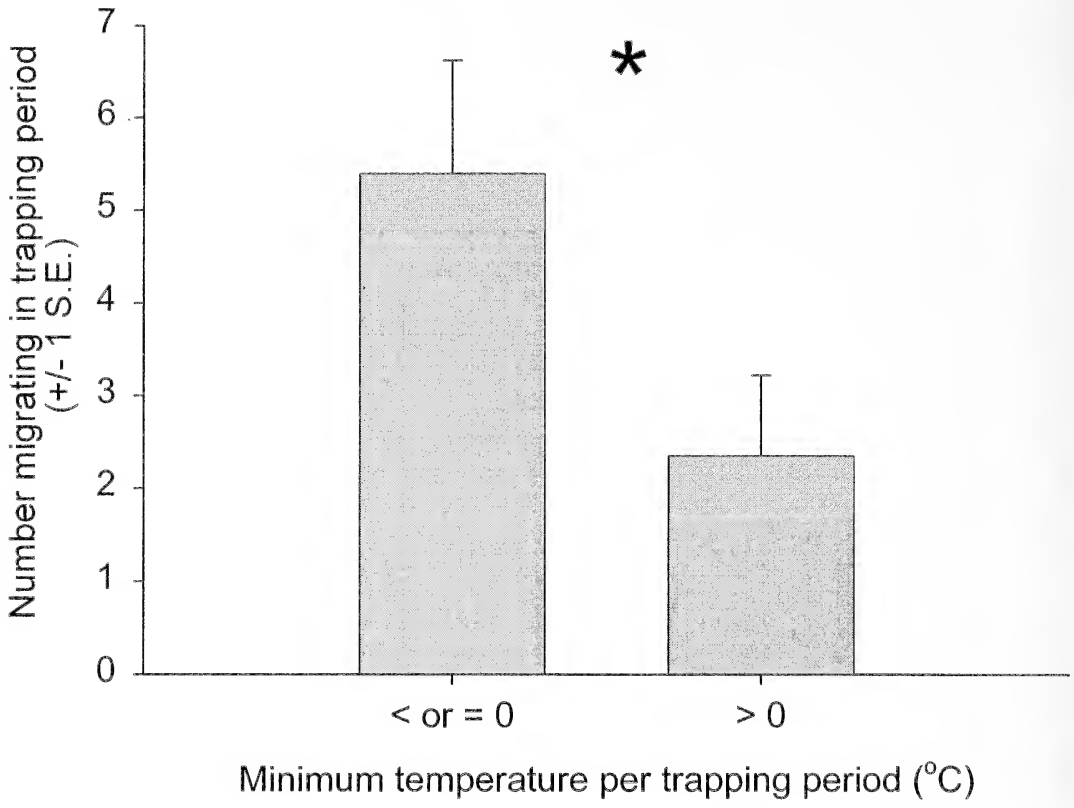

Figure 2.—Comparison of number of spiders (+ S.E.) captured at drift fences during trapping periods with minimum temperatures above freezing (0 °C) versus at freezing and below (1996–1999). Asterisk indicates significant differences between categories at $P < 0.05$.

tested for substrate choice in 1997; 74 escaped before choice was recorded and none failed to make a choice. In 1997 and 1999, a total of 37 and 42 spiders collected from the forest drift fences were tested for substrate choice; 4 escaped before choice was recorded in 1997, no spiders escaped in 1999. No spiders in either year failed to make a choice after the 3 h acclimation period. For the field experiments on substrate choice in 1997 and 1999, substrate choice was not predicted by month collected, orientation of substrate, or whether the individual had migrated (1997 only), (logistic regression, $P > 0.05$ in all cases). There was a marginal effect of year on the probability of choosing leaves ($x^2 = 3.51$, $df = 1$, $P = 0.06$). The proportion of individuals choosing leaves over cobble varied over the experimental period in both 1997 and 1999. Spiders collected from the forest in 1997 and 1999 showed an increase in leaf choice in the experimental arenas when migration occurred in the field, discounting the 2 Nov. movements forced by storm-driven beach inundation (Figs. 3, 4). In 1997, the beach-captured individuals increased their leaf choice in late October, before migration occurred in the field (Fig. 3).

Table 1.—Average daily temperature (°C) and variance in 1999 at four microhabitat sites at the beach-forest interface: under leaves, under cobble, ambient shade, and ambient sun.

Microhabitat	Daily temperature	Variance
Leaves	7.2	1.4
Rocks	6.4	9.4
Shade	6.2	8.0
Sun	6.2	7.8

Spiders collected from the beach chose cobble significantly more often than leaves in every set of substrate choice experiments (23 total), both in the field and laboratory (x^2 test for goodness of fit, Bonferroni-adjusted, k =

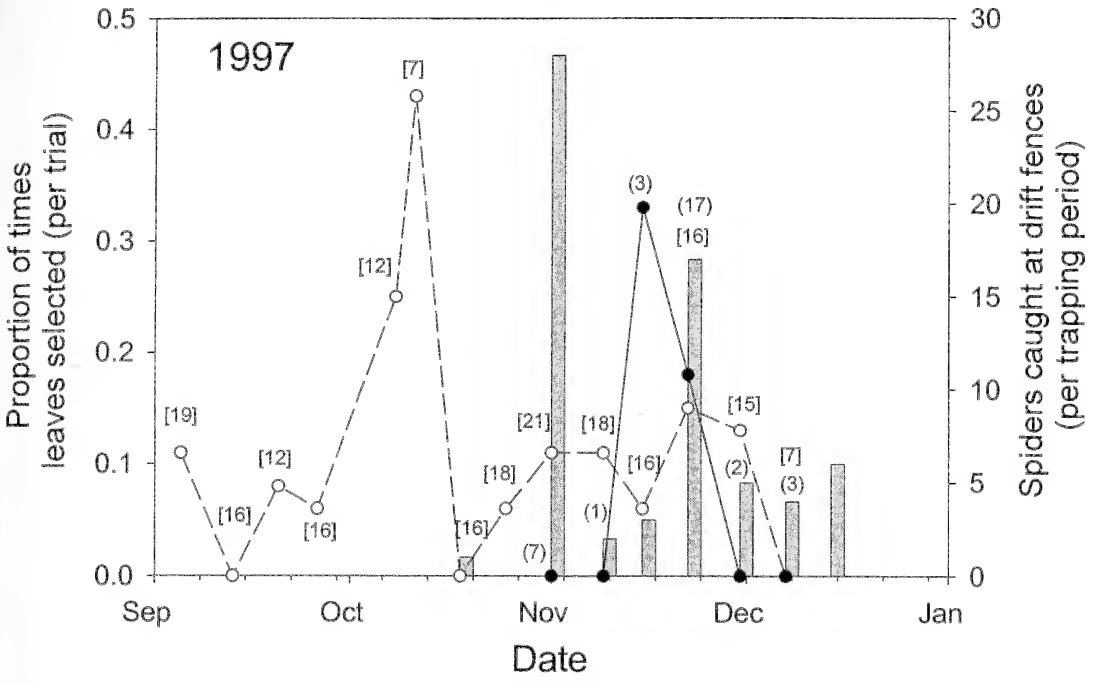

Figure 3.—Results of field substrate choice trials in 1997 showing how substrate choice changes with migratory tendency. Open circles = substrate preference of spiders captured on beach, closed circles = substrate preference of spiders captured at drift fences, and bars = number of spiders captured in drift fences over season. Sample size for substrate choice experiments above each data point: number of spiders captured on beach in brackets, number captured at drift fence in parentheses.

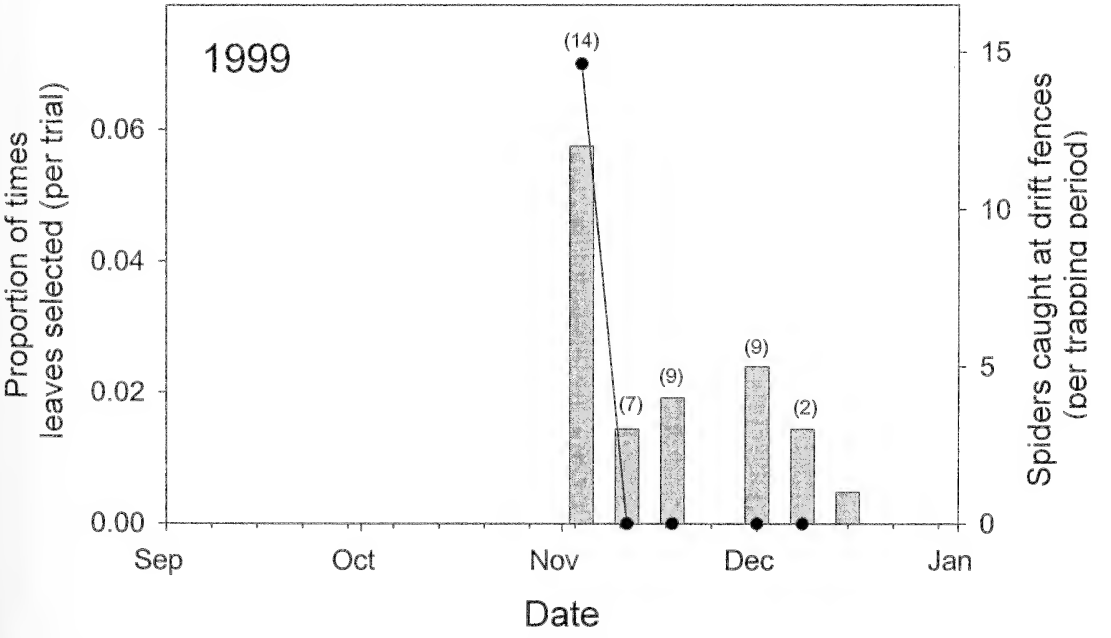

Figure 4.—Results of field substrate choice trials in 1999 showing how substrate choice changes with migratory tendency. Closed circles = substrate preference of spiders captured in drift fences, and bars = number of spiders captured in drift fences over season. Sample size for substrate choice experiments above each data point.

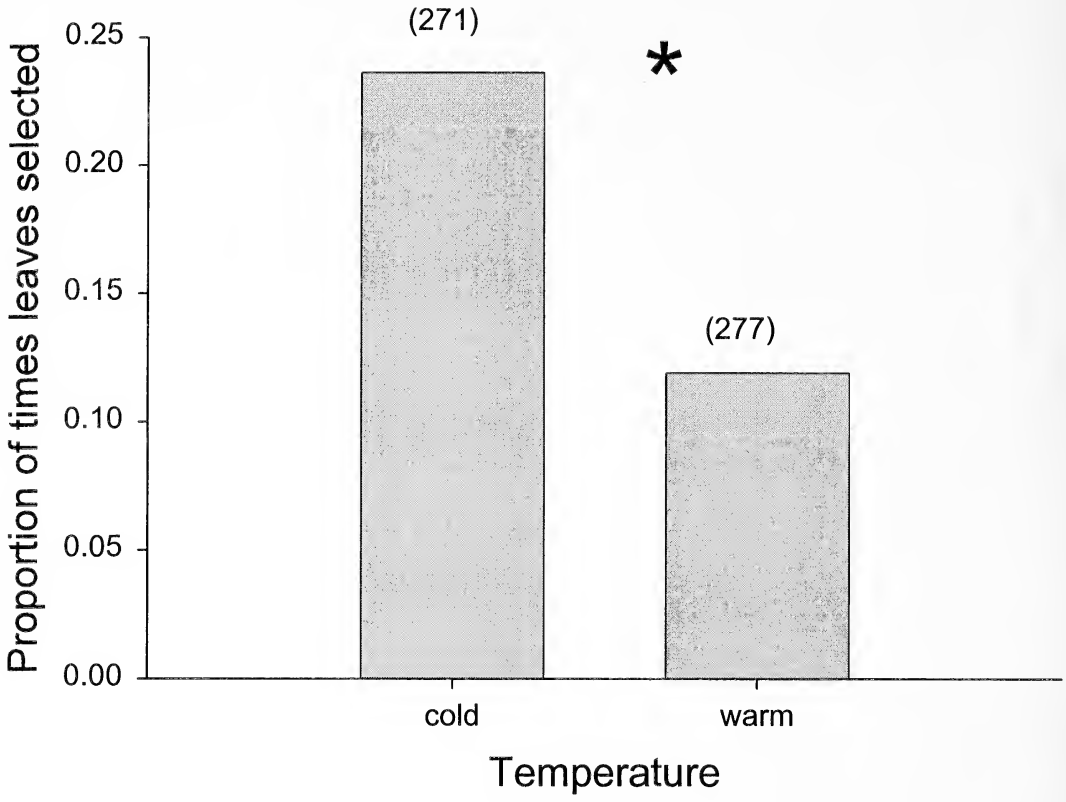

Figure 5.—Laboratory experiments on beach-captured spiders in 1997, showing effect of temperature collected on substrate choice. Sample size for each data point in parentheses. Asterisk indicates significant differences between temperatures at $P < 0.05$. The interaction between temperature and data collected not significant.

23, $P < 0.002$ for every week's trial). Weekly sample sizes of the forest-captured individuals often were inadequate for analysis (n = 1–18) because the replicates were limited by the numbers that were caught in pitfall traps that week, but the pooled yearly results showed that the vast majority also selected cobble (29 of 33 in 1997; 41 of 42 in 1999), both highly significantly different from a 50:50 ratio ($x^2_{1,1}$ = 12.5, 20.0; $P < 0.001$, < 0.001: x^2 tests for goodness of fit).

Substrate choice in the laboratory.—A total of 604 spiders were tested in the laboratory experiment over the 5 sample dates. There were 56 deaths or escapes and 6 incidents in which the spider apparently made no choice, 29.4 ± 2 spiders were tested per treatment with the exceptions of 4 treatments that contained only 19 or 20 replicates. Those treatments, late November/warm short and long daylength, and September/cold short and long daylength, had reduced replicates due to alternate use of the spiders and an experimental error. The main effects of temperature and collection date on substrate choice were significant (temperature x^2 = 9.24, df = 1, P = 0.002; collection date x^2 = 10.6, df = 4, P = 0.03). Preference for leaves peaked in cold conditions and for spiders collected in Oct. (Figs. 4, 5). Post-hoc pairwise contrasts revealed that spiders collected in Oct. had a significantly different substrate preference from those collected in Dec. (Bonferroni adjusted P-value, $P < 0.005$) and were marginally different from those collected in early and late November ($P < 0.05$). Photoperiod did not significantly affect substrate choice ($P > 0.05$). The two-way and three-way interactions among photoperiod, temperature and collection date were also not significant ($P > 0.05$).

Temperature and date collected significantly affected whether an individual molted or fed (Table 2). The incidence of molting and feed-

Table 2.—Proportion of spiders molting and feeding during laboratory experiments in 1999. Molting and feeding are significantly affected by temperature and collection date. Sample sizes in parentheses.

	Proportion molting		Proportion feeding	
Collection date	Cold	Warm	Cold	Warm
OCT 5–7	0.02 (66)	0.35 (66)	0.50 (66)	1.00 (66)
NOV 4–7	0.00 (62)	0.02 (64)	0.56 (66)	1.00 (64)
NOV 21–23	0.00 (62)	0.03 (40)	0.21 (42)	1.00 (40)
DEC 12–15	0.00 (63)	0.00 (61)	0.10 (63)	0.66 (61)

ing decreased over the season and occurred more often in warm conditions (for molting: temperature $x^2 = 46.0$, $df = 1$, $P < 0.001$, date $x^2 = 59.1$, $df = 4$, $P < 0.001$; for feeding: temp $x^2 = 291.9$, $df = 1$, $P < 0.001$, date $x^2 = 108.1$, $df = 4$, $P < 0.001$). Photoperiod had no effect (for molting: $x^2 = 0.4$, $df = 1$, $P > 0.05$, for feeding: $x^2 = 1.1$, $df = 1$, $P > 0.05$).

DISCUSSION

Seasonal migration.—*Photoperiod and temperature:* Our use of drift fence captures as a measure of directional migration and not general activity is supported by the lack of drift fence captures in early fall when warm weather increases activity, the large disparity between spiders caught in front and behind the drift fences (greater than 70% captured in front), and the low recapture rate of spiders in fences (3% in 1997). The timing of *P. lapidicina* movement and the numbers of spiders moving from the cobble beach to the adjacent forest as measured by the drift fences varied among years (Fig. 1). Date of peak movement occurred between early November and late December (S.D. = 15.5 d) during 1996–1999, which is at least 1.5 times as variable as the timing of seasonal migration in some fish and birds (S.D. = 2–10 d; Comeau et al. 2002). For most seasonal responses in arthropods, photoperiod is used to cue the physiological changes that determine the timing of major life history events (Tauber et al 1986). Many organisms use absolute day length (Tauber et al. 1986; Delisle & McNeil 1987), change in day length (Beck 1980) or both to differing degrees (Han & Gatehouse 1991), to anticipate seasonal changes in their environment. The high variance in timing of migration over the years argues against a singular role of photoperiod in this system, but it seems unlikely that photoperiod played no role in migration given its seasonal nature.

It appears that temperature has an effect on migration: low temperatures may thus increase the migratory response of *P. lapidicina* to seasonal change, while mild temperatures decrease it. Only about half as many spiders were captured at the drift fences during the relatively warm autumns of 1998 and 1999 (the 82nd and 96th coldest of the past 100 years), as during the relatively cold autumns of 1996 and 1997 (the 19th and 34th coldest; NOAA, 1996–1999). Furthermore, a greater number of spiders migrated during weeks when temperatures dipped below freezing, perhaps to avoid contact with ice on the beach (Schaeffer 1977), although minimum ambient temperature did not correlate with movement. During mild winters, more individuals apparently overwinter on the very edge of the cobble-forest boundary (< 5 m into forest) or on the beach itself (Morse 1997). Although it is unclear what their relative survival is compared to those that migrate, if these spiders continue feeding on the beach it could give them a size advantage at the beginning of the following season. Ultimately, retreating to leaves during colder seasons may afford the spiders protection from extreme conditions because of the less variable temperatures in the microhabitat under leaves. Leaf litter has been previously found to be a preferred microhabitat for spiders in the winter because of its low thermal conductivity and temperature fluctuation (Schaeffer 1977)

Other temperate zone arthropods exhibit seasonal responses to low temperatures (Delisle & McNeil 1987; Han & Gatehouse 1991; Eubanks & Miller 1992). For example, the length of the prereproductive periods of true armyworm moths *Pseudaletia unipuncta* (Delisle & McNeil 1987) and oriental armyworm moths *Mythimna separata* (Han & Gatehouse 1991), which determine their predisposition to

migrate in the autumn, increase under cold temperature or short photoperiod regimes. These responses suggest that cold temperature may directly determine an animal's propensity to migrate. The mechanism for temperature driving this propensity may be either direct, by affecting rates of growth and development, or indirect, by inducing a physiological syndrome that prepares the insect for coming seasonal changes (Tauber et al. 1986).

Rainfall, humidity and storm events: Seasonal change in habitat preference of non-burrowing lycosids has been previously documented in temperate forests. Eubanks & Miller (1992, 1993) suggested that the habitat shift of *Gladicosa pulchra* in the late summer and early fall was affected by rainfall (surrogate for soil humidity). Rainfall and ambient humidity appeared to have no influence on the habitat preference of *P. lapidicina*. This difference may be explained by the geographical ranges of the two populations. *Gladicosa pulchra* was studied in the southern U.S., where winters are much milder, and desiccation has a larger probability of affecting survival. In addition, the fresh water flowing across portions of our study sites would further reduce dessication risk for the spiders.

Storm events did not correlate with movement in the field. However, the large early peak in 1997 (on 2 Nov., 28 individuals were captured) occurred after a large storm in which the tide inundated the high beach (J.M. Kraus & D.H. Morse, pers. obs.).

Substrate choice as a proxy for migration?—We expected that if substrate preference did play a role in spider migratory decisions, that spiders would be more likely to choose leaves after they had migrated. This expectation was not met: in 1997, 4 out of 29 (14%) spiders that had migrated and 24 of 185 (13%) that had not migrated chose leaves. Although the overall proportion of individuals choosing leaves was not affected by migratory status, it appears that individuals captured at the drift fences show their highest leaf preference within a week of peak migration, not including storm forced movements in 1997 (Figs. 3, 4). On the other hand, beach-captured spiders chose leaves most frequently a month prior to peak migration (1997, Fig. 3).

We predicted that spiders that had not yet migrated would exhibit a strong preference for leaf substrate during the fall migration. Although being in migratory condition does not necessarily result in preference for leaf litter, since spiders that have already migrated still chose cobble a majority of the time, the peak in preference for leaf litter coincided with high migration rates over two years. This result suggests that migration is somehow associated with substrate preference. Collectively, the field-conducted substrate choice experiments, coupled with the pattern of migration, suggests that change in substrate preference is related to seasonal movement from beach cobble to forest leaf litter in the field. To verify this connection, similar comparisons need to be made over more years, using a larger number of replicates.

Month of collection and substrate orientation had no effect on spider substrate choice in the field. The marginal effect of year on substrate choice in the field is most likely attributable to the small number of replicates in 1999.

Substrate choice and environmental cue.—The results of the laboratory substrate choice experiments suggest that temperature, which may affect the number of individuals migrating in the field, also influenced individual substrate preference. Individuals maintained at cold temperatures selected leaf substrate significantly more often than those kept at warm temperatures (Fig. 5). There are two possible explanations for this pattern. Spiders in cold conditions may simply choose the warmer substrate (leaves), especially if they have not yet acclimated to cold temperatures in the field. Alternatively, the spiders may have been physiologically primed, perhaps by photoperiod in the field, to respond to cold temperatures by changing their substrate preference. An additional condition in which the substrate was cooled before being placed with warm spiders or warmed before being placed with cooled spiders, would have allowed us to establish whether the spiders were undergoing a physiological change that affected their preference or if they were simply responding to the tactile cues they were receiving at that moment. Given that the spiders decreased feeding and molting as the season progressed (Table 1), and the main effect of date collected on spider choice (leaf preference peaked in Oct., Fig. 6), we suggest that a physiological change had occurred and the spiders' choices

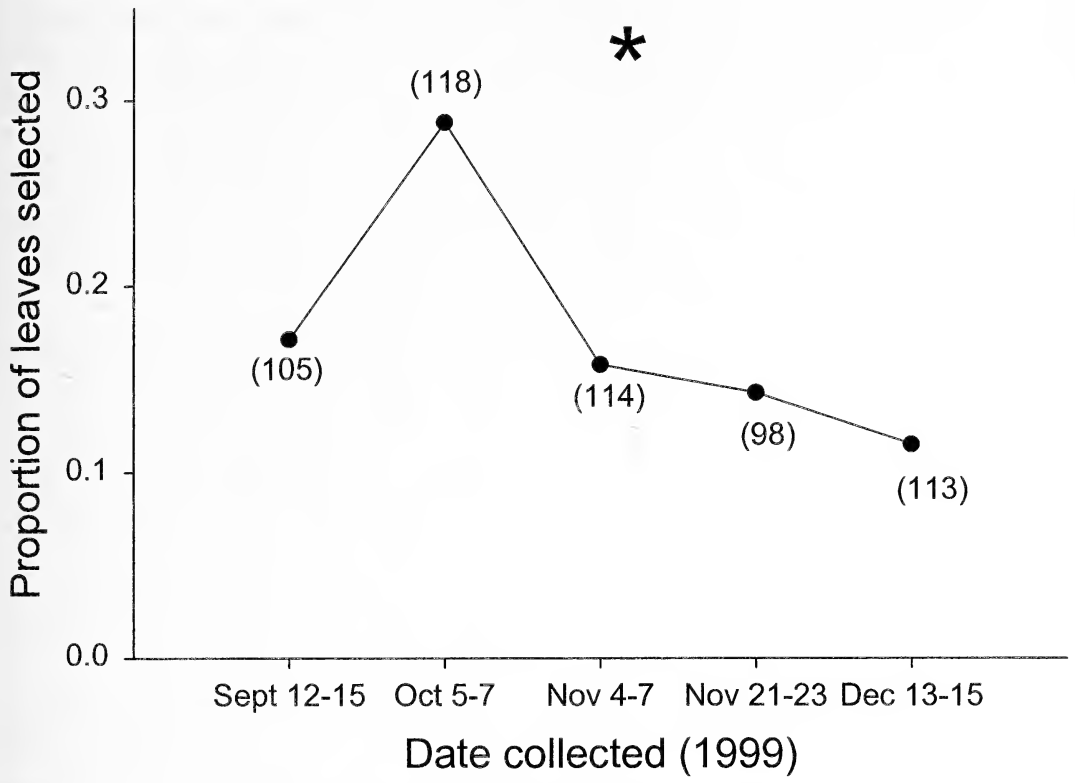

Figure 6.—Laboratory experiments on beach-captured spiders in 1999, showing effect of date collected on substrate choice. Sample size for each data point in parentheses. Asterisk indicates significant differences between dates at $P < 0.05$.

were most likely driven by an interaction between physiological and tactile factors.

Photoperiod showed no effect on substrate preference in our laboratory experiments. This result was surprising because of the role that photoperiod traditionally has played in triggering physiological changes that allow temperate organisms to respond to the onset of winter (Tauber et al. 1986; Kumar 1997). It is possible that *P. lapidicina* do not use photoperiod to make substrate choice decisions. Alternatively, the experimental design may not have tested an aspect of photoperiod (such as change in day length) to which the spiders respond, or the 8 d acclimation period at the beginning of the experiment was inadequate. There is some evidence for the latter explanation, since the date at which spiders were collected from the field affected substrate choice in the laboratory (Fig. 6). Spiders collected in October were almost twice as likely to choose leaves in the laboratory as those collected at any other time. Apparently the spiders were at least partially making their substrate choice decisions based on conditions in the field.

On the failure of some individuals to migrate.—The striking difference between the rocky intertidal and adjacent forest litter may inhibit *P. lapidicina* that encounter the interface from moving across the boundary. Since the spiders were born on the beach in the spring and early summer (Morse 1997), they are naïve to the forest environment, having previously experienced no more than occasional leaves. This background is consistent with leaves never being favored by a majority of individuals in the experiments, even though they provide a less variable temperature regime than the beach cobbles.

Although we have not quantified costs of migrating to the leaf litter, we have trapped both arachnid and shrew predators at the drift fences (Morse 1997 pers. obs.). In other communities prey moving across habitat boundaries have been shown to enhance the num-

bers of predators there (Polis & Hurd 1996; Hering & Platcher 1997; Henschel et al. 2001). This cost may inhibit movement for *P. lapidicina*. Spiders may also continue to reap a benefit from access to food on the beach. Laboratory data suggest, however, that this benefit would be most significant early in the season, since the spiders undergo a two-fold decline in overall feeding rate and cease molting as the season progresses, even if maintained in warm temperatures (Table 1). Further, individuals captured on the beach during November and December are slightly lighter than ones caught in the forest (J.M. Kraus pers. obs.) and have ceased gaining mass by this time (D.H. Morse pers. obs.).

Depending on the year, most of the spiders may eventually cross the beach-forest interface, but some do not unless driven to it by physical factors such as ice and high water. Although they might change their choices with experience and time, the performance of the naïve individuals is the relevant variable here, since it represents the normal condition for an individual first encountering the habitat boundary.

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SPATIAL DISTRIBUTION AND MICROHABITAT PREFERENCE OF *PSECAS CHAPODA* (PECKHAM & PECKHAM) (ARANEAE, SALTICIDAE)

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ABSTRACT. Although spiders generally do not have a strong association with the plants on which they live, the jumping spider *Psecas chapoda* inhabits and breeds on *Bromelia balansae* (Bromeliaceae). To understand the relationship between *Psecas chapoda* and *Bromelia balansae*, we investigated whether the type of habitat (forest or grassland), the size of the bromeliad and the inflorescence of the host plants affected the preference and/or density of *P. chapoda*. We also examined how spiders of different ages and their eggsacs were distributed on the leaf layers of the rosette of host plants and whether *P. chapoda* used other plants in addition to *B. balanasae*. *Psecas chapoda* occurred with higher frequency on bromeliads in grasslands to those in forest. In grassland, larger bromeliads had more spiders, but this was not true of bromeliads in the forest. This spider avoided bromeliads with inflorescence. Most of the spiderlings (70%) occurred in the central layer of the rosette leaves, and their distribution pattern suggested that they sought shelter to protect themselves from desiccation or cannibalism, both of which are commonly observed in this species. Older spiders, as well as females without eggsacs, occurred in the external layers whereas 90% of the females with eggsacs occurred close to the central layers. Deposition of the eggsacs near the center of the rosette can allow the spiderlings to reach their shelter rapidly and to be less exposed to desiccation and cannibalism. The non-detection of *P. chapoda* on non-bromeliad plants, and the stereotyped behaviors on the host-plant suggest that this jumping spider was strongly associated with *B. balansae*.

Keywords: Animal-plant interaction, habitat selection, microhabitat, plant architecture, Salticidae

In contrast to host-specific herbivorous insects (Schoonhoven et al. 1998), spiders generally do not have a strong association with the plants on which they occur. However, some spider species inhabit and breed on specific plants and interact indirectly with their hosts (Louda 1982; Figueira & Vasconcellos-Neto 1991, 1993; Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2004). Why some spiders choose specific plants and how the occurrence of such spiders affects the organization of spider communities are important aspects in understanding the community structure on a given host plant and in elucidating the direct and indirect interactions within and among species (Abraham 1983; Uetz 1991). The components of habitat reported to influence the numbers and types of spiders include the abundance and richness of prey (Riechert & Tracy 1975; Waldorf 1976; Rypstra 1983; Miller & Drawer 1984; Schmalhofer 2001), the availability of extrafloral nectarines as a food source and as foraging sites (Ruhren & Handel 1999), the availability or density of sites for constructing webs (Lubin 1978; Rypstra 1983; Greenstone 1984; Herberstein 1997; Figueira & Vasconcellos-Neto 1991), the availability of foraging sites (Scheidler 1990; Romero 2001; Schmalhofer 2001; Romero & Vasconcellos-Neto 2003), the spatial distribution of web and foraging sites (Greenquist & Rovner 1976; Robinson 1981; Louda 1982) and the availability of sites for shelter (Riechert & Tracy 1975; Gunnarsson 1990, 1996) and breeding (Smith 2000).

The jumping spider *Psecas chapoda* (Peckham & Peckham 1894) (Salticidae), previously identified as *P. viridipurpureus* Simon 1901 by Rossa-Feres et al. (2000), is commonly found on *Bromelia balansae* Mez. (Bromeliaceae) and has an apparently host-specific distribution. This plant does not store rainwater in its rosette. *Psecas chapoda* spends its entire

reproductive cycle: courtship, mating, ovisac formation and populational recruitment of the young spiders on this plant (Rossa-Feres et al. 2000). Females produce 1–3 eggsacs on the concave side of the central region of the leaves. The eggsacs are enveloped with a plain silk cover and are spun at the edge of each leaf. Since females remain under this cover and on the eggsacs (Fig. 1) (Rossa-Feres et al. 2000), there may be maternal care of the offspring.

In this study, we examined the spatial and microspatial patterns of *P. chapoda* on *B. balansae* and investigated the factors affecting this distribution. Specifically, we assessed whether the type of habitat (forest or grassland) and the size and architecture (absence vs. presence of inflorescences) of the bromeliad affected the density of *P. chapoda*. We also determined whether spiders of different ages and the eggsacs were randomly distributed among the leaf layers of the rosette, and whether *P. chapoda* was associated exclusively with *B. balansae*.

METHODS

This work was done in a fragment of semideciduous forest (250 m x 60 m) and in an adjacent grassland area along the margin of a river, in the city of Dois Córregos (22° 21′ S, 48° 22′ W), São Paulo state, southwestern Brazil, from July 1998–May 2000 and in March and April 2002. Only *Bromelia balansae*, a ground-dwelling bromeliad (Figs. 2–4), occurs in the study area.

Habitat preference.—Habitat preference was determined by recording the number of *P. chapoda* on *B. balansae* growing in the forest and in the grassland. Observations were made in the cold-dry season (July 1998), at the beginning of the rainy season (October 1998), in the hot-rainy season (February 1999) and at the end of the rainy season (April 1999), along two parallel 250 m transects in the forest and grassland (one each). The two transects were at least 20–30 m apart, and 37–53 stalks of *B. balansae* in the forest and 75–103 stalks in the grassland were randomly chosen in each season. The spider density per bromeliad stalk was compared between the forest and grassland transects and among the four seasons using two-way ANOVA. Since the occurrence of the spiders may be skewed by the density of bromeliads, the number of plants growing at 10 m intervals in 100 m x 6 m transects of forest and grassland was estimated to determine if there were variations in density between sites. Since the preference for bromeliads was affected by the presence of inflorescence, only bromeliads without inflorescence were included in the analysis (see below).

Influence of host plant size on the microhabitat preference.—To examine the preference of spiders for host plants of different sizes, the relationship between the bromeliad surface area and the number of *P. chapoda* was examined for bromeliads in grassland, at the forest margin and within the forest. The bromeliads (50–82 in grassland, 16–27 at the forest margin and 31–53 within the forest) were observed bimonthly from July 1998–July 1999. The bromeliads were randomly chosen in each sample period. Bromeliads growing under tree branches but which received incident solar light at any time of the day were considered to occur in the forest margin. The total surface area was estimated by multiplying the surface area of one leaf by the total number of green leaves on each bromeliad. The leaf surface area was estimated using the formula: length (L) x breadth (B) of a leaf from the middle layer of the rosette, chosen at random, x 1/2. Linear regression analysis was used to assess the relationship between surface area and the number of spiders. Student t-test was used to compare the bromeliad surface area between grassland and forest.

Influence of inflorescence on spider density.—The relationship between *B. balansae* inflorescence and spider density was examined by comparing the density of spiders on grassland *B. balansae* with and without inflorescence (Figs. 2–4). The observations were made in December 1998 and 1999 because almost all of the *B. balansae* at the study sites bloomed in this season. The results were analyzed using the G-test.

Preference for leaf layers.—*Bromelia balansae* has several leaf layers in the rosette (Figs. 2, 3). Since preliminary observations showed that *P. chapoda* was distributed in different layers of the rosette according to the spiders' age, the distribution patterns of spiders of different ages were determined by examining 24–64 grassland bromeliads with at least five leaf layers. The observations were


1
2
3
4

made bimonthly, from November 1999–May 2000. The bimonthly interval of observations was determined to avoid data dependence (i.e., temporal pseudoreplication, Hurlbert 1984), since spiders change instars by molting and the eggsacs are constructed and abandoned in approximately one month (Rossa-Feres et al. 2000; G.Q. Romero pers. obs.). Age-specific patterns of spots and coloration were used to classify *P. chapoda* as spiderlings (3rd instar), young (4th and 5th instars), and juvenile males (up to 1.1 cm in body length) or females (6th instar). Although sex-specific patterns of spots and coloration are also useful for discriminating subadult and adult stages, subadult and adult females with the same spot and coloration patterns and of similar size (up to 1.6 cm in body length) are difficult to distinguish in the field. In addition, the number of subadult males is extremely small. For these reasons, we created two additional groups, namely subadult (7th instar) + adult females (8th instar) and adult males (8th instar) (Rossa-Feres et al. 2000; G.Q. Romero pers. obs.). In the subadult and adult female class, the adult females with eggsacs were distinguished from subadult and adult females without eggsacs. The distributions of the five developmental stages above and those of subadult and adult females with and without eggsacs were analyzed using the G-test.

Selectivity of *P. chapoda* for the host plant.—The selectivity of *P. chapoda* for *B. balansae* was examined in March and April 2002, a period of high spider density, by the following three methods: 1) Direct observation; searching for spiders, silk shelters and abandoned eggsacs on 590 non-bromeliad plants belonging to the families Asteraceae, Fabaceae, Solanaceae, Asclepiadaceae, Lauraceae and several grasses. The plants examined were 10–170 cm tall and grew at least 3 m away from *B. balansae*. At each observation, we examined the abaxial and adaxial sides of leaves and branches. 2) Beating or shaking the plants with a stick. The spiders were collected on a beating tray, essentially a cloth-covered frame that sloped slightly towards the center (Southwood 1978). All of the spiders dropping off non-bromeliad plants (up to 170 cm tall) were collected. Fifty plants were sampled in grassland, 50 at the forest margin and 50 within the forest. Five beats per sample (plant) were done between 1:00–4:00 p.m. 3) Pitfall traps; 30 pitfall traps (10 cm in diameter and 15 cm deep) containing 75% ethanol were placed among individuals (0.4–1.5 cm) of *B. balansae*. The spiders were collected five days after the traps were placed. Voucher specimens of *P. chapoda* were deposited in the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo.

RESULTS

Habitat preference.—The average number of *P. chapoda* on *B. balansae* was significantly greater in grassland than in forest (two-way ANOVA, $F_{1,534} = 123.67$, $P < 0.0001$, Fig. 5). The average number of *P. chapoda* on *B. balansae* also changed seasonally (two-way ANOVA, $F_{3,534} = 2.89$, $P = 0.035$) and was lower in the hot, rainy season (Fig. 5). The interaction between the factors habitat and seasonality was significant ($F_{3,534} = 2.82$, $P = 0.038$). There was no difference between the density of bromeliads in grassland and forest (T-test, $t = -0.46$, 18 df, $P = 0.648$).

Influence of host plant size on the microhabitat preference.—There were positive, significant relationships between bromeliad surface area (size) and number of spiders inhabiting the plant, in the grassland and forest margins (Table 1). Despite the bromeliads in the forest being bigger than the bromeliads in the grassland (data from July 1998; forest: 9649.0 cm^2 ± 1256.2 (SE), grassland: 4609.5 ± 470.6 (SE); $t = -4.53$, 154 df, $P < 0.001$), there were no relationships between plant size and number of spiders in the forest (Table 1). Up to 21 spiders were seen on a single plant in the grassland area, whereas a maximum of 3 spiders was seen on bromeliads in the forest.

Influence of inflorescence on spider density.—Among bromeliads with no inflores-

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Figures 1–4.—1. Female of *P. chapoda* (arrowhead) under the plain silk cover and on the eggsac produced on a leaf of *B. balansae*. 2. Individual of *B. balansae* in vegetative phenophase in the grassland. 3. In the beginning of inflorescence release (note the central leaves folding back). 3. with presence of infrutescence. (Photos: G.Q. Romero).

Table 1.—Linear regressions of the relationship between the bromeliad size (surface area) and individuals number of *Psecas chapoda* in the grassland, forest margins and into the forest, in different seasons.

	Places	Equations	n	r^2	*F*	*P*
1998						
Jul	Grassland	Y = 0.00033X + 1.44	82	0.51	84.67	<0.001
	Margin	Y = 0.000102X + 0.94	21	0.27	7.06	0.016
	Forest	Y = 0.0000013X + 0.63	53	0.0003	0.02	0.899
Sep	Grassland	Y = 0.00011X + 1.11	76	0.09	7.22	0.009
	Margin	Y = 0.000031X + 0.86	22	0.04	0.77	0.390
	Forest	Y = 0.0000006X + 0.28	53	0.0001	0.001	0.932
Nov	Grassland	Y = 0.00045X + 1.27	74	0.08	6.70	0.012
	Margin	Y = 0.000084X + 0.74	27	0.06	1.51	0.231
	Forest	Y = 0.000002X + 0.31	48	0.001	0.06	0.806
1999						
Jan	Grassland	Y = 0.00055X + 0.89	67	0.22	18.64	<0.001
	Margin	Y = 0.000047X + 1.92	18	0.01	0.25	0.623
	Forest	Y = 0.000002X − 0.56	43	0.0009	0.04	0.849
Mar	Grassland	Y = 0.00021X + 1.40	62	0.07	4.28	0.043
	Margin	Y = 0.00024X + 0.34	20	0.28	7.07	0.016
	Forest	Y = 0.000013X + 0.33	36	0.04	1.29	0.264
May	Grassland	Y = 0.00067X + 0.38	50	0.47	43.05	<0.001
	Margin	Y = 0.00021X + 0.19	24	0.37	12.77	0.002
	Forest	Y = 0.000029X + 0.20	36	0.11	4.22	0.048
Jul	Grassland	Y = 0.00017X + 1.50	53	0.08	4.16	0.047
	Margin	Y = 0.00011X + 0.25	16	0.31	6.17	0.026
	Forest	Y = 0.000005X + 0.35	31	0.003	0.08	0.783

cence, 79% and 90% were occupied by *P. chapoda* in 1998 and 1999, respectively. In contrast, for bromeliads with inflorescences, only 17% and 13% were used by *P. chapoda* in 1998 and 1999, respectively. The percentage of bromeliads used by *P. chapoda* was significantly different between stalks with and without inflorescences (Fig. 6).

Preference for leaf layers.—Spiderlings occurred only in the first three central layers of the rosettes of *B. balansae*. Their distribution among the three layers was not random ($G = 30.60$, 2 df, $P < 0.0001$), and most spiderlings (70%) occupied the first layer in the center of the plant (Fig. 7). Although young spiders occurred on plants with five or more layers, 50% of this age interval was observed in the second layer ($G = 114.90$, 4 df, $P < 0.0001$, Fig. 8). Juvenile males and females were not found in the first layer and used the other layers randomly ($G = 5.03$, 3 df, $P = 0.170$, Fig. 9). The random use of all layers except for the first one was also observed for adult males ($G = 1.80$, 3 df, $P = 0.615$, Fig. 10). In the case of subadult and adult females, more than 40% occurred in the third layer ($G = 43.20$, 4 df, $P < 0.0001$, Fig. 11). The distribution patterns of spiders among the leaf layers was different between adult females with eggsacs and subadult and adult females without eggsacs. More than 90% of the females with eggsacs occupied the second and the third layers ($G = 18.70$, 2 df, $P < 0.0001$), while the subadult and adult females without eggsacs occurred in the third, fourth and fifth layers with higher frequencies ($G = 22.65$, 4 df, $P = 0.0001$, Fig. 12). Only one adult or subadult female occupied the first layer.

Selectivity of *P. chapoda* for the host plant.—No individuals of *P. chapoda* or their vestiges (silk shelters and abandoned eggsacs) were found on 590 non-bromeliad plants close to *B. balansae* individuals. Although many spiders (~400 individuals) belonging to several families, including 6–7 Salticidae species, were collected by beating non-bromeliad plants and in pitfall traps on the ground between the stalks of *B. balanasae*, no *P. chapoda* were found. In three years of observations, only three adult *P. chapoda* males were observed on the ground and one young was

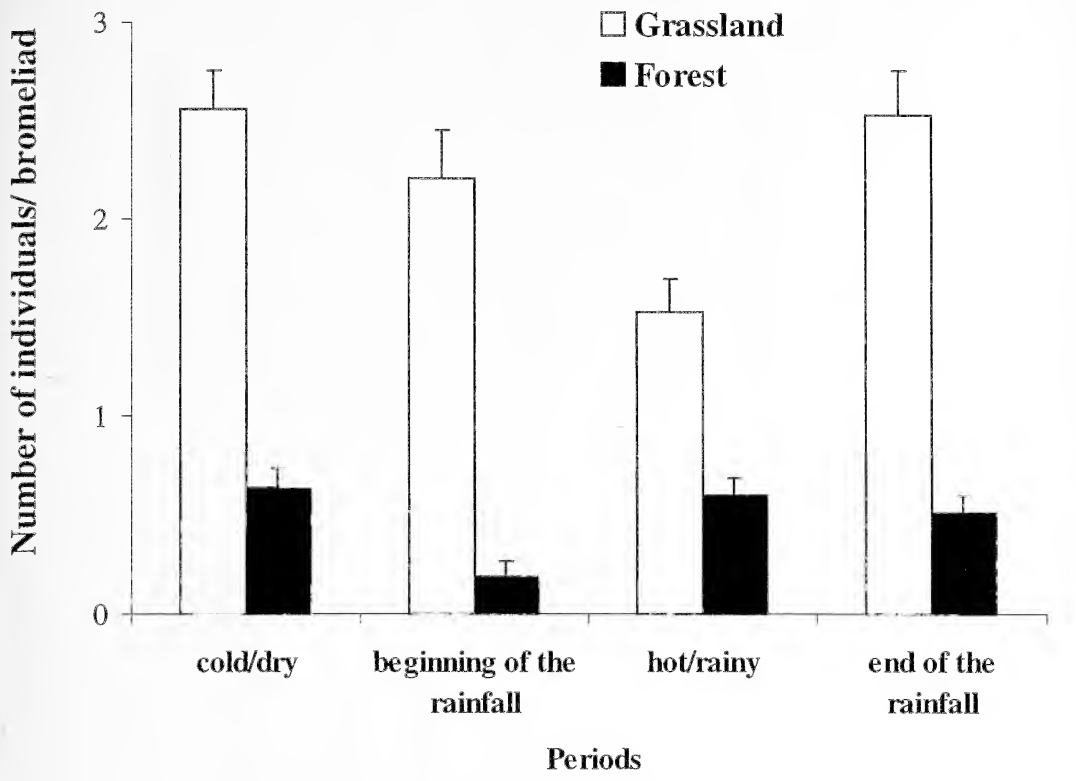


Figure 5.—Seasonal variation in the mean density of *Psecas chapoda* individuals on *Bromelia balansae* in grassland (open bars) and in forest (black bars). The sampled periods were: cold/dry = July 98, beginning of the rainfall = October 98, hot/rainy = February 99, end of the rainfall = April 99. Error bars are ± 1 SE.

seen on a gramineous leaf close to *B. balansae* in grassland.

DISCUSSION

Although several studies have shown that spiders of the family Salticidae may select certain microhabitats (Crane 1949; Richman & Whitcomb 1980; Jackson 1986; Cutler 1992; Cutler & Jennings 1992; Johnson 1995; Jackson & Li 1997; Taylor 1998), the distribution of *P. chapoda* on *B. balansae* and the absence of this species on non-bromeliad plants and in pitfall traps around bromeliads suggested a strong relationship between *P. chapoda* and *B. balansae*. The courtship, mating, deposition of eggsacs and populational recruitment of *P. chapoda* occur on *B. balansae*. *Psecas chapoda* also used *B. balansae* throughout the year at Sao José do Rio Preto (SP), about 200 km from the present study site (Rossa-Feres et al. 2000). Moreover, this spider species was collected and photographed (female) on *B. balansae* in Beni, Bolivia (Höfer & Brescovit 1994: picture 2a; H. Höfer, pers. comm.). In addition, *P. chapoda* was observed on *B. balansae* in 26 cities of three Brazilian states and in one locality of Paraguay (G.Q. Romero, unpubl. data). Thus, *P. chapoda* seems to be strictly associated with *B. balansae* in a large geographic range.

Our results show that *P. chapoda* preferred bromeliads in grassland to those in forest, and that bigger bromeliads were preferred more in grassland, whereas such a relationship between plant size and the average number of spiders was not observed in forest bromeliads. When the bromeliads are approached by an observer, *P. chapoda* on the leaf layers quickly jump towards the bottom of the rosette in a stereotyped jumping behaviour (G. Q. Romero, personal observation). The internal base of the rosette of bromeliads serves as a refuge and shelter from desiccation, as well as a resting place (G.Q. Romero, pers. obs.). In the forest, the bromeliads receive a large number of dry leaves from trees growing nearby and

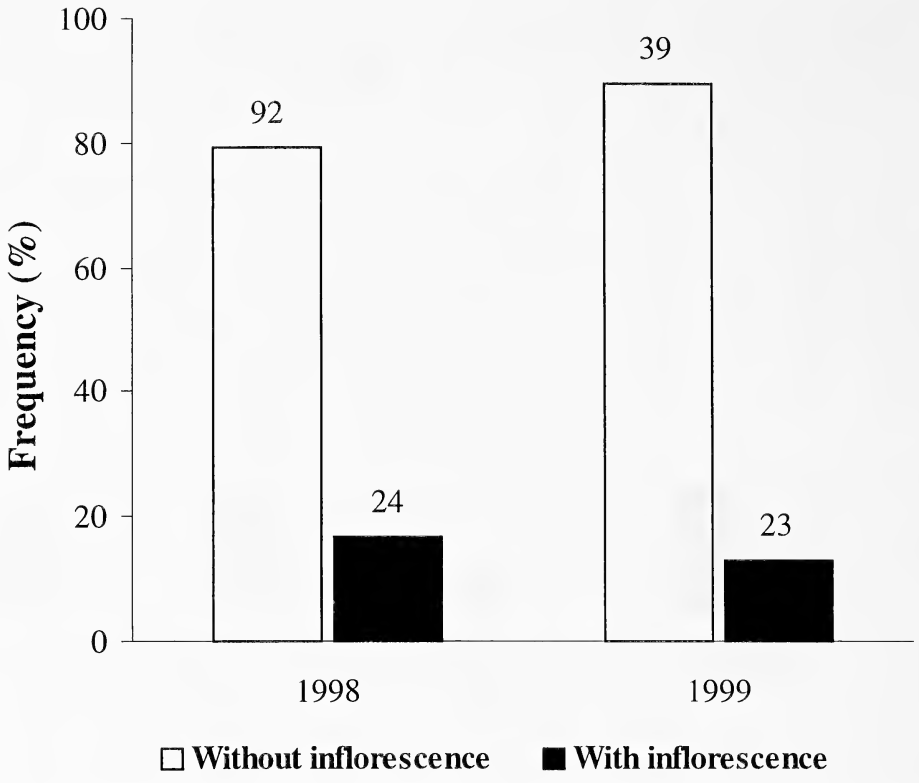
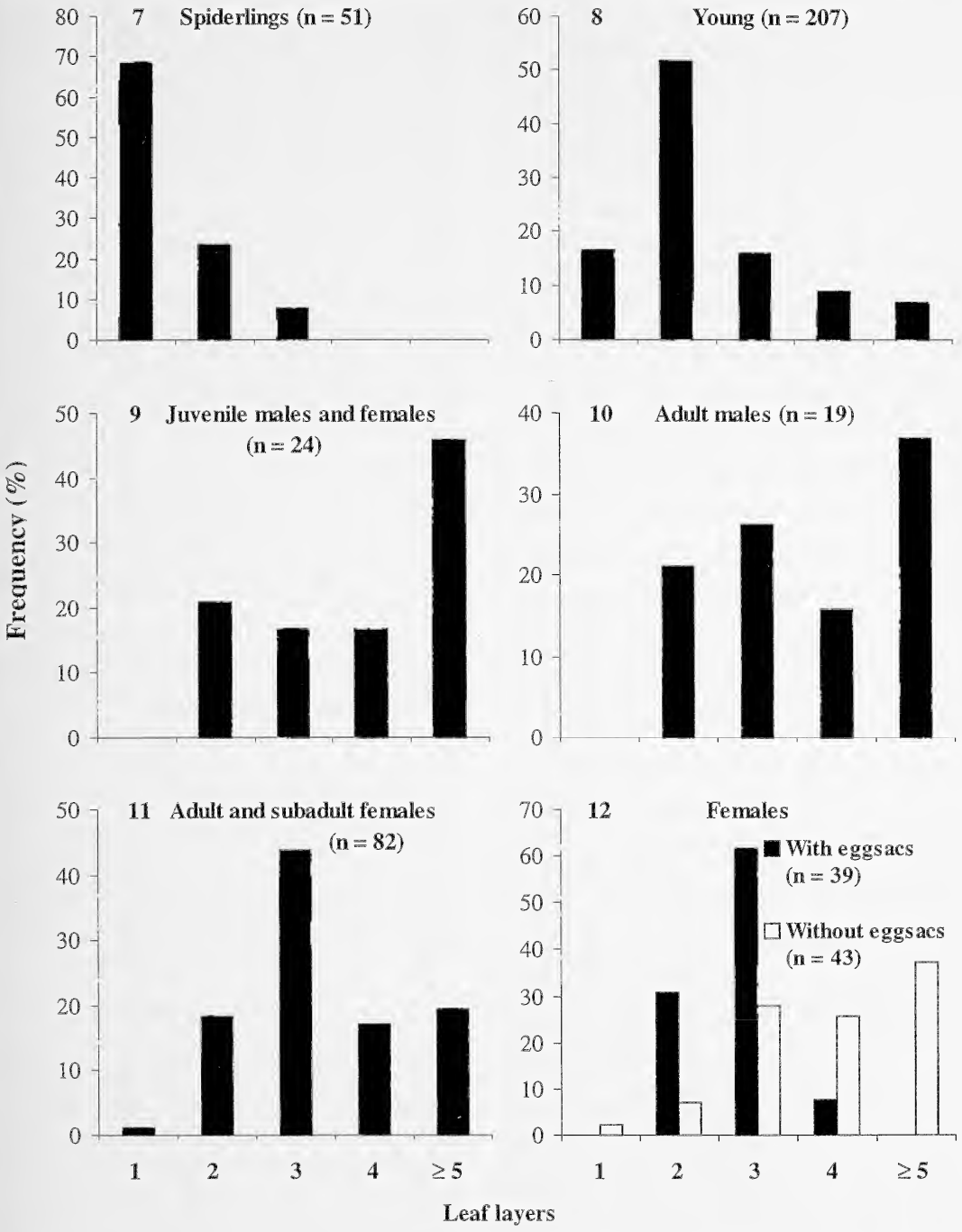


Figure 6.—Frequency of bromeliads with and without inflorescence occupied by *Psecas chapoda*, in December 1998 and 1999. The values above the bars indicate number of bromeliads examined. G-test with Yates' correction (G_{1998} = 13.6, 1 df, $P < 0.001$; G_{1999} = 15.6, 1 df, $P < 0.001$).

these leaves form a compact humic mass that fills completely the internal base of the bromeliad rosettes, regardless of the difference in size. Since a large quantity of dry leaves at the bottom of the rosette hampers the use of this microhabitat, *P. chapoda* appears to prefer grassland bromeliads which gather few or no dry leaves compared to forest bromeliads.

Larger bromeliads had more individuals of *P. chapoda*. Larger plants have a larger surface area available for foraging and many leaf layers in their rosettes for shelter, which can support more spiders. Generally, spiders that inhabit larger bromeliads consist of one adult male, one or two adult females frequently with eggsacs and several young and spiderlings, probably offspring of these resident females. In contrast, little, peripheral bromeliads are frequently occupied by young, juveniles and subadult spiders (G.Q. Romero, pers. obs.). Adult females probably choose larger bromeliads to obtain more food and shelter for their offspring, decreasing the probability of intraspecific competition and/or cannibalism. Since salticids have good eyesight (Foelix 1982; Foster 1982), they can obtain more food on larger leaves. Figueira & Vasconcellos-Neto (1993) showed a strong relationship between the size of the *Paepalanthus bromelioides* (Eriocaulaceae) rosette and prey availability, and between the size of the *P. bromelioides* rosette and the weight and/or reproductive success of *Latrodectus geometricus* Koch 1841 (Theridiidae). According to these authors, larger plants offered a larger number of prey for *Latrodectus* females so that females grew rapidly and produced more eggs.

In addition to the size of *B. balansae*, the presence of inflorescence also affected the abundance of *P. chapoda* since almost all spiders occurred on bromeliads without inflorescence. During the reproductive period of *B. balansae*, the green color of the central parts (leaves) of the rosette changes to red prior to inflorescence blooming. At the same time, the leaves fold back and extend parallel to the ground (Fig. 4) probably to expose the flowers



Figures 7–12.—Distribution of *Psecas chapoda* individuals with different age class (7–11) and of adult females with eggsacs vs. adult + subadult females without eggsacs (12) in the leaf layers of the *Bromelia balansae* rosette (see text for the definitions of layers).

to pollinators. These changes alter the plant architecture from a conical tridimensional configuration to a flattened, almost bidimensional one. Since the leaves do not touch each other even at this time because of the geometric conformation of the plant, the surface area of the leaves of bromeliads remains constant, even after the blooming season. How-

ever, the change in plant architecture affects the availability of shelter and breeding sites, and the spiders are exposed to external factors such as predation and climatic conditions. Some jumping spiders are able to find and catch prey in tridimensional and topographically complex environments (Hill 1979; Tarsitano & Andrew 1999). If *P. chapoda* also prefers bromeliads with a tridimensional arrangement, the preference for bromeliads without inflorescence could be explained by differences in the shelter and breeding sites and by architectural changes in the host plants.

Although most arthropods in the tropics show peak numbers in the hot, rainy season (see Wolda 1988), *P. chapoda* was more abundant in the cold, dry season and at the end of the rainy season. Many grass species around bromeliads grow rapidly in the rainy season and may cover part of the bromeliads. Although additional studies on the causes of the high density of *P. chapoda* in the cold, dry season are necessary, the abundance of grasses may affect the availability of food for the spiders, and may influence the amount of contact between male and female spiders, as well as the colonization of bromeliads.

In some spider species there are differences in the choice of microhabitat among adults and immatures in order to facilitate prey capture and to avoid predation (Edgar 1971). It is possible that *P. chapoda* may show age-specific use of bromeliads.

Approximately 70% of the *P. chapoda* spiderlings occurred in the first central layer of the *B. balansae* rosette. Since the leaves extend vertically in the first layer, they overlap each other to form a cylinder of small diameter. Small spiderlings can use this microhabitat to shelter from desiccation and/or cannibalism by larger spiders. Young spiders, one or two instars older than the spiderlings, and which still need a place to shelter, occurred more frequently in the second layer of the rosette because of the difficulty in reaching the first layer, that has very narrow and clumped leaves. Juvenile males and females of a similar size to the adults were generally restricted to outer layers.

The value of the central rosette as a nursery for spiderlings was also suggested by the different distribution of females with and without eggsacs. Almost all of the females with eggsacs (90%) occurred between the second and third layers, whereas females without eggsacs were more common in the outer layers (Fig. 12). When females with eggsacs remained at the center of the rosette, the hatched spiderlings easily reached the first layers and the probability of cannibalism was reduced. Several studies have shown that during oviposition, the females of insects choose plants that enhance the performance of their offspring (see Schoonhoven et al. 1998). Females of *P. chapoda* remained over their eggsacs (Rossa-Feres et al. 2000), indicating that there was more than one type of maternal investment in offspring in this species. According to Richman & Jackson (1992), such maternal behavior is very common, if not universal, in the Salticidae, and presumably deters predators and parasitoids of the eggs. These results suggest that the distance from the ovisac to the center of the bromeliad may influence the type of maternal behavior seen. Desiccation and cannibalism can represent selective pressures that influence the choice of breeding sites by females and this may affect the survival of the offspring after leaving the nest.

In conclusion, *P. chapoda* was associated with *B. balansae* from grassland. This spider occurred in very low frequency on bromeliads from forest and those from grassland with presence of inflorescence. The specific behaviors of *P. chapoda* on the plant and the absence of detection of this species on non-bromeliad plants suggest a strict association between *P. chapoda* and *B. balansae*.

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A REVIEW OF THE TASMANIAN SPECIES OF PARARCHAEIDAE AND HOLARCHAEIDAE (ARACHNIDA, ARANEAE)

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ABSTRACT. The Tasmanian species of Pararchaeidae and Holarchaeidae are revised and higher species-group relationships within the Pararchaeidae are examined. Three new species of *Pararchaea* Forster are described and the genitalia of *P. corticola* Hickman, *P. ornata* Hickman, *P. saxicola* Hickman and *P. bryophila* Hickman are redescribed, the receptacula of *P. ornata*, *P. saxicola* and *P. bryophila* for the first time. The male of *P. ornata* is newly described. With the addition of *P. hickmani* new species, *P. lulu* new species and *P. robusta* new species, the Tasmanian pararchaeid fauna is enlarged to include seven species. *Holarchaea globosa* (Hickman) is rediagnosed and the female genitalia and male are described and illustrated for the first time. Biological information is included where known.

Keywords: Tasmania, *Pararchaea*, *Holarchaea*, taxonomy, new species, Australia

The Pararchaeidae and Holarchaeidae are monogeneric families of small (0.8–3.2 mm), entelegyne, araneomorph spiders, known only from Australia and New Zealand (Forster & Platnick 1984). Both groups belong to the widely-known, tetrafamilial 'archaeid assemblage', sharing with the Afrotropical, Malagasy and Australian Archaeidae and the New Zealand and Chilean Mecysmaucheniidae an anterior cephalothoracic foramen completely surrounding the cheliceral bases (Forster & Platnick 1984). While probably more diverse, and clearly more widespread in the past (with two genera of fossil Archaeidae known from European Baltic amber), the four families together form a relatively speciose clade of extant palpimanoid spiders. Certainly, only a small proportion of the Australian species of *Pararchaea* Forster, and the New Zealand species of *Holarchaea* Forster, are currently named, despite extensive collections present in museums. This work is a contribution to the task of elucidating this rich alpha-diversity, reviewing in full the known pararchaeid and holarchaeid spider species of Tasmania. Higher species-group relationships within the Pararchaeidae are also examined, and biological information is summarized for all taxa where known.

The Pararchaeidae and Holarchaeidae share similar, largely linked, taxonomic histories. The first species in both families were described by Forster (1949), with *Pararchaea rubra* (Forster 1949) initially placed in the genus *Zearchaea* Wilton 1946 and *Holarchaea novaeseelandiae* (Forster 1949) in the genus *Archaea* Koch & Berendt 1854; both taxa were included in the family Archaeidae. The genera *Pararchaea* and *Holarchaea* were subsequently erected by Forster (1955), the former expanded to include the generic type *P. alba* Forster 1955 from New Zealand and *P. binnaburra* Forster 1955 from the Lamington Plateau, south-eastern Queensland. Forster (1955: 398) noted that "the close relationship shown between the Australian species *P. binnaburra* and *P. alba* is of great interest in that it provides yet another indication of the close affinity of a section of the Australian cryptozoic fauna with that of New Zealand." Four more species of Australian *Pararchaea* were described by Hickman (1969) from Tasmania, followed by the holarchaeid *Holarchaea globosa* (Hickman 1981), from south-western Tasmania. Forster & Platnick (1984) erected the monogeneric, entelegyne families Pararchaeidae and Holarchaeidae, along with the Mecysmaucheniidae and the newly delimited Archaeidae, recognizing the heterogeneous nature of the four taxa. Thus the Archaeidae (formerly a generic 'dumping ground' for taxa for over 100 years) was finally restricted to include, among extant taxa, only three genera from South Africa, Madagascar and mainland

Figures 1–2.—*Pararchaea* species: 1. *P. ornata*, holotype female, dorsal view, showing abdominal coloration; 2. *P. saxicola*, allotype female, dorsal view. Note the clearly procurved posterior margin of the pars cephalica on both specimens.

Australia, all united by haplogyne genitalia and an extreme elevation of the pars cephalica (Forster & Platnick 1984).

METHODS

All specimens were described and illustrated in 75% ethyl alcohol, or from scanning electron micrographs. Female genitalia were cleared in lactic acid. Digital photographs were taken through binocular and compound microscopes and cleared epigynes were temporarily mounted on glass cavity slides with 100% glycerine. All measurements are in millimetres and taken from camera lucida projection. All illustrations are by the author.

Abbreviations.—AME = anterior median eyes; ALE = anterior lateral eyes; ALS = anterior lateral spinnerets; DS1 = dorsal sigillum 1 (anterior left); DS2 = dorsal sigillum 2 (anterior right); DS3 = dorsal sigillum 3 (posterior right); DS4 = dorsal sigillum 4 (posterior left); DSP1 = dorsal sigilla pair 1 (anterior); DSP2 = dorsal sigilla pair 2 (posterior); DSQ = dorsal sigilla quadrangle; PME = posterior median eyes; PLE = posterior lateral eyes; PMS = posterior median spinnerets; PLS = posterior lateral spinnerets; PTA = peg tooth group A; PTB = peg tooth group B; PTC = peg tooth group C; SEM = scanning electron micrograph; TAS = Tasmania; VS1 = ventral sigillum 1 (anterior left); VS2 = ventral sigillum 2 (anterior right); VS3 = ventral sigillum 3 (posterior right); VS4 = ventral sigillum 4 (posterior left); VSP1 = ventral sigilla pair 1 (anterior); VSP2 = ventral sigilla pair 2 (posterior); VSQ = ventral sigilla quadrangle.

Specimens examined are located in the following repositories: Australian Museum, Sydney (AMS); Queensland Museum, Brisbane (QM); Queen Victoria Museum, Launceston (QVM); Museum of Victoria, Melbourne (VICM).

SYSTEMATICS

Family Pararchaeidae Forster & Platnick

Pararchaeidae Forster & Platnick 1984: 65.

Type genus.—*Pararchaea* Forster, by original designation.

Diagnosis.—The Pararchaeidae can be distinguished from all other spider families by chelicerae arising from a distinct, ventrally sclerotized foramen (as in Archaeidae and Mecysmaucheniidae), in combination with entelegyne female genitalia (Forster & Platnick 1984). Pararchaeid spiders can also be recognized by having the combination of the following characters: anterior tarsi longer than metatarsi, stout peg teeth on the distal prolateral chelicerae, non-reduced female pedipalps, squamate cephalothoracic cuticle with hairs only on the pars-cephalica and a distinctively procurved posterior margin to the pars-cephalica in dorsal view (Figs. 1, 2).

Distribution.—The Pararchaeidae are known only from Australia and New Zealand. Within Australia, numerous specimens have been collected from north-eastern, middle-eastern and south-eastern Queensland, eastern

New South Wales, Victoria, Tasmania and southwestern Western Australia.

Remarks.—Spiders of the family Pararchaeidae are most similar in body form and size to certain Mecysmaucheniidae, namely *Aotearoa magna* (Forster 1949) from New Zealand. If the number of spinnerets on the latter is noted, however (*Aotearoa* with two spinnerets, *Pararchaea* with six), then the Pararchaeidae is unlikely to be confused with any other Araneae, especially in Australia where mecysmaucheniid spiders are apparently absent.

Pararchaea Forster 1955

Pararchaea Forster 1955: 397; Hickman 1969: 3; Forster & Platnick 1984: 71.

Type species.—*Pararchaea alba* Forster 1955, by original designation.

Diagnosis.—As for family.

Generic description.—In part from Forster & Platnick 1984.

Cephalothorax: Carapace, when viewed laterally, rhomboidal. Pars cephalica rising steeply from pars thoracica above level of coxae III or IV; highest centrally or posteriorly, sloping towards eyes. Viewed dorsally, carapace rounded or oval with rounded lateral indentations; posterior, procurved margin of pars cephalica appearing clearly demarcated from rest of carapace (Figs. 1 & 2). Carapace cuticle squamate, without tubercles or mounds. Eight eyes in two rows; laterals pearly-white, contiguous, widely separated from medians; AME closely spaced, dark-colored; PME pearly-white, well separated from each other and AME. Carapace mainly devoid of hairs, except on dorsal and dorso-lateral aspect of pars cephalica and around eyes and clypeus. Anterior margin of carapace encircling bases of chelicerae, with sclerotized cuticle extending ventrally to form antero-ventrally-facing oval foramen. Ventral suture below foramen completely or incompletely fused with sclerotized cuticle; if latter with thin longitudinal division. Clypeus extending antero-ventrally in front of eyes; longest medially (forming dorsal margin of foramen). Lateral margins of pars-thoracica smoothly indented, with or without small (separate) triangular inter-coxal sclerites projecting ventrally between coxae; the latter meeting and sometimes fusing with sternal projections. If without intercoxal sclerites, carapace either fused to or separate from sternum. Sternum not much longer than wide, posteriorly obtuse; cuticle squamate, usually fused with posterior carapace around petiole. Maxillae directed across labium; serrula a single row of teeth. Labium triangular, wider than long; not rebordered.

Chelicerae: Paturon relatively long, sometimes elongate, proximally constricted; cuticle finely reticulated or squamate. Pronounced keel extending down ventral surface of paturon; originating about a third of length from proximal end, continuing to behind distal tip of non-extended fang. Fang relatively short, strongly curved. Pored cheliceral gland mound situated between distal end of keel and tip of non-extended fang; in some species associated with ridged spur. Promargin adjacent to fang with three groups (PTA, PTB, PTC) of stout peg teeth, each tooth with raised socket basally; PTA with 5–6 contiguous teeth directly adjacent to non-extended fang; PTC with 3 larger teeth on promargin of outer surface; PTB with 1–3 teeth between PTA and PTC. Outer surface of paturon of males with or without transverse stridulatory ridges. Retrolateral surface of paturon with strong, smooth, moveable hairs (erected upon full opening of chelicerae).

Legs and female pedipalp: Legs (longest to shortest: 4, 1, 2, 3) relatively short, cuticle squamate, clothed with slender serrate or smooth hairs; no spines or scopulae. Single trichobothrium on metatarsi, 2–4 on tibiae; bothria well developed with smooth posterior hood. Tarsi longer than metatarsi (excluding Leg IV of some species), with three claws; upper claws with single row of teeth, inferior claw with single medial tooth. Tip of tarsi with modified serrate hairs; base sometimes distinctly swollen. Tarsal organ capsulate. Femur I usually with proximal, dorsally curved row of retrolateral denticles; in some species forming an apparent stridulatory mechanism with prolateral file on femur II. Female pedipalp entire, without claw; usually with several long, stiff hairs prolaterally.

Abdomen: Abdomen, when viewed dorsally, broadly oval without tubercles. Cuticle coriaceous; clothed with short to long smooth or serrate hairs. Petiole encircled by sclerotized cuticle; often extending posteriorly on males to cover epigastric region and anterior face of abdomen (forming anterior sclerite). Small to

large, variably-shaped dorsal scute present on males. Dorsal abdomen with anterior (DSP1) and posterior (DSP2) pair of oval or circular, small (DS1 & DS2) to large (DS3 & DS4) sigilla, forming quadrangle (DSQ) antero-centrally. Ventral abdomen also with anterior (VSP1) and posterior (VSP2) pair of subequal, circular sigilla (VS1–4), forming quadrangle (VSQ) centrally. Internal darkened sclerotic invaginations usually visible around tracheal opening and along posteriorly-converging lines either side of VSQ. Book lung covers and external epigyne of females separately sclerotized; intromittent pores surrounded by an epigynal sclerite. Post-epigastric sclerites present on males and females; small and square or triangular on females, significantly enlarged and usually fused to anterior sclerite on males. Six spinnerets, fully developed; surrounded ventrally and/or dorsally by separate sclerites, or encircled by sclerotized cuticle. Posterior tracheal opening situated closely anterior to colulus, surrounded by extended spinneret sclerite, or by separate tracheal sclerite on females of most species. Colulus small, conical, with two posteriorly projecting hairs.

Male genitalia: Epiandrous glands composed of spigots arising in clusters either side of genital opening; spigots with shared, raised sockets. Male palpal patella and tibia without processes. Cymbium spoon-shaped with prominent retrolateral apophysis (paracymbium) proximally, of variable (usually distinctive) shape. Bulb large, extending over full length of cymbium; embolus spinous, arising from base and curving around prolateral margin of bulb. Sclerotized distal plate situated over bulb, distal to base of embolus; usually complex with one or more apophyses and ornate cuticular microstructure.

Female genitalia: Epigyne with pair of separate (although sometimes broadly touching), thick-walled, variously lobed receptacula, composed of internal systems of ducts and chambers; a single distinct fertilization duct leads from each receptaculum into bursal cavity, bending outwardly or prolaterally (often only visible when cleared epigynes are viewed laterally).

Included species.—*Pararchaea alba* Forster 1955, *P. binnaburra* Forster 1955, *P. bryophila* Hickman 1969, *P. corticola* Hickman 1969, *P. hickmani* new species, *P. lulu* new species, *P. ornata* Hickman 1969, *P. robusta* new species, *P. rubra* (Forster 1949), *P. saxicola* Hickman 1969.

Key to the Tasmanian species of *Pararchaea*

1. Males 2
   Females 8
2. Dorsal abdomen with distinctive anterior cardiac stripe and posterior chevrons ..... *Pararchaea ornata* Hickman
   Dorsal abdomen not patterned as above 3
3. Retrolateral femur I with dorsally curved row of proximal denticles; proximal tarsus I not distinctly swollen; postero-dorsal aspect of pars cephalica without medial indentation ... 4
   Retrolateral femur I without dorsally curved row of proximal denticles; proximal tarsus I distinctly swollen; postero-dorsal aspect of pars cephalica with medial indentation (Fig. 10) ..... *Pararchaea bryophila* Hickman
4. Dorsal scute small, not extending posterior to level of DSP2 5
   Dorsal scute large, extending posterior to level of DSP2 6
5. Dorsal scute roughly circular (Fig. 16) ..... ***Pararchaea hickmani*** new species
   Dorsal scute very small, transversely elongate (Fig. 11) ..... *Pararchaea saxicola* Hickman
6. Dorsal scute longitudinally elongate, pale in color (Fig. 22); paracymbium distally 'star-shaped' (Fig. 21) ..... ***Pararchaea lulu*** new species
   Dorsal scute roughly as long as wide, dark brown in color; paracymbium not distally 'star-shaped' 7
7. Cymbium with retrolateral lobe-like extension at base of paracymbium (Fig. 12); paracymbium with two divergent apophyses; post-epigastric sclerites not extending posterior to level of VSP1 ..... *Pararchaea corticola* Hickman
   Cymbium without retrolateral lobe-like extension at base of paracymbium; paracymbium

a single, distally rounded, curved projection (Fig. 26); post-epigastric sclerites extensive, extending posterior to level of VSP1 (Fig. 28) ..... ***Pararchaea robusta*** new species

8. Retrolateral femur I with dorsally curved row of proximal denticles 9
   Retrolateral femur I without dorsally curved row of proximal denticles ..... *Pararchaea bryophila* Hickman
9. External epigyne distinctive, as illustrated in Fig. 8 ..... *Pararchaea corticola* Hickman
   External epigyne not as illustrated in Fig. 8 10
10. Dorsal abdomen with distinctive anterior cardiac stripe and posterior chevrons (Fig. 1) .. *Pararchaea ornata* Hickman
    Dorsal abdomen not patterned as above 11
11. Receptacula large, 'comma-shaped', broadly touching along inward margins (Fig. 6) .... *Pararchaea saxicola* Hickman
    Receptacula otherwise 12
12. Receptacula oval-shaped, posteriorly convergent (Fig. 5) .. ***Pararchaea robusta*** new species
    Receptacula otherwise 13
13. Receptacula with prominent, 'nose-like' inward lobes (Fig. 4); abdomen without 'marbled' coloration in life ..... ***Pararchaea lulu*** new species
    Receptacula without prominent, 'nose-like' inward lobes (Fig. 3); abdomen with 'marbled' coloration in life ..... ***Pararchaea hickmani*** new species

Pararchaea bryophila Hickman 1969 (Figs. 7, 9–10)

Pararchaea bryophila Hickman 1969: 9, figs. 25–30; Schütt 2000: 137, figs. 2, 6, 7, 10.

Type material.—Holotype male, Punch Bowl Reserve, Launceston, Tasmania, Australia, 41°25′S, 147°7′E, 24 August 1929, moss, V.V. Hickman (AMS KS 6633). Allotype female, same data as holotype (AMS KS 6634).

Other material examined.—AUSTRALIA: *Tasmania*: 1 ♂, 1 ♀, Launceston (AMS KS 54300); 1 ♀, Point Sorell (QVM 13: 17998); 1 ♀, no locality data (QVM 13: 23869); 1 ♂, 1 ♀, northeast TAS (AMS KS 25985); 1 ♂, King River (AMS KS 65966); 1 ♂, West Downs via Ridgely (AMS KS 66072); 2 ♀, same data (AMS KS 66078); 1 ♀, Dip River Falls (AMS KS 66038); 1 ♀, ~3 km S of Waratah Junction on Murchison Hwy (AMS KS 66088); 2 ♂, Punch Bowl Reserve, Launceston (AMS KS 28721); 1 ♂, 2 ♀, same data (AMS KS 54295).

Diagnosis.—Male and female *P. bryophila* can be distinguished from all other known Tasmanian congeners by the absence of retrolateral denticles on the femur of leg I and their small size.

Description.—*Male (AMS KS 66072):* Pedipalp (Fig. 9): paracymbium large, 'sickle-shaped', with two divergent projections. Distal plate with two prominent, pro-distally directed apophyses.

Female (QVM 13: 17998): Epigyne (Fig. 7): receptacula posteriorly convergent, together forming 'V-shape'; each receptaculum with 'nose-like' inward lobe.

Distribution and habitat.—*Pararchaea bryophila* appears to be widespread in Tasmania. Hickman (1969) recorded that the types were collected from moss.

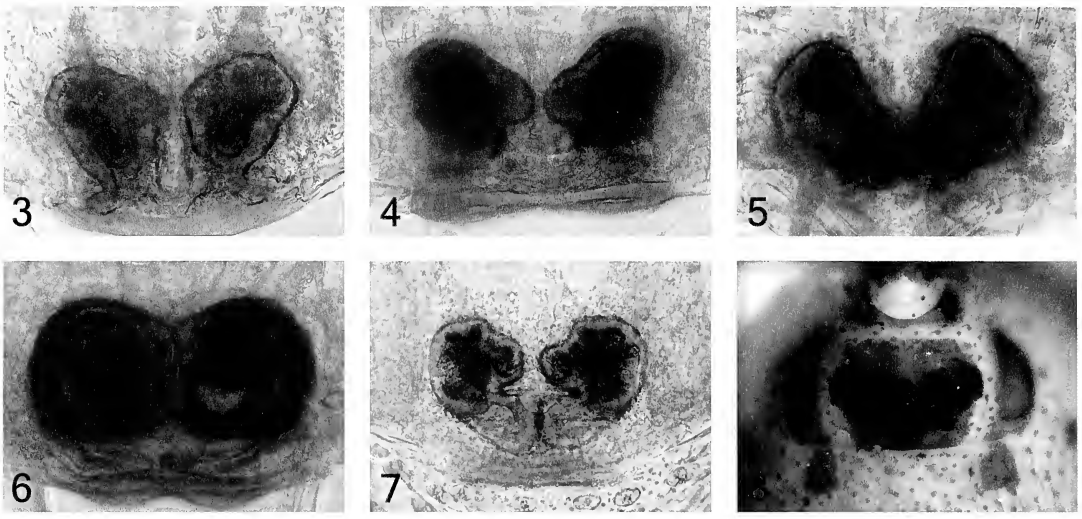
Pararchaea corticola Hickman 1969 (Figs. 8, 12)

Pararchaea corticola Hickman 1969: 3, figs. 10–15.

Type material.—Holotype male, The Queen's Domain, Hobart, Tasmania, Australia, 42°52′S, 147°19′E, 24 May 1937, under the loose bark of eucalypts, V.V. Hickman (AMS KS 6635). Allotype female, same data as holotype except March 1955 (AMS KS 6636).

Diagnosis.—Female *P. corticola* can be distinguished from all other known Tasmanian congeners by the large size and the characteristic shape of the external epigyne (Fig. 8). Males can be distinguished from all other known Tasmanian congeners by the retrolateral lobe-like extension on the cymbium (at base of paracymbium; Fig. 12), and the presence of an oval sclerite surrounding VSP2.

Description.—*Male (holotype AMS KS 6635):* Pedipalp (Fig. 12): paracymbium large, with two divergent apophyses. Cymbium with retrolateral, lobe-like extension at base of paracymbium. Distal plate extended distally to



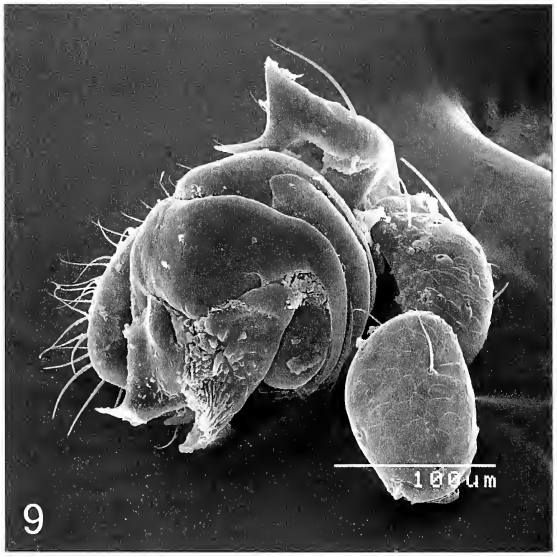
Figures 3–8.—Epigynes of *Pararchaea* species: 3–7. Cleared receptacula, dorsal view. 3. *P. hickmani*; 4. *P. lulu*; 5. *P. robusta*; 6. *P. saxicola*; 7. *P. bryophila*; 8. *P. corticola*, allotype female external epigyne, ventral view.

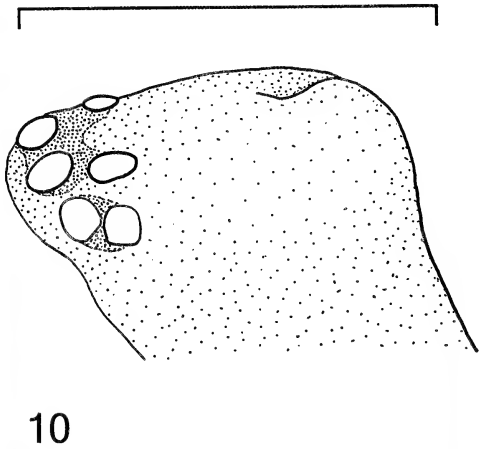
form prominent 'conductor' around tip of embolus.

Female (allotype AMS KS 6636): Epigyne (Fig. 8): as the allotype was the only female specimen of this species examined, the epigyne was not dissected. The external appearance is, however, characteristic, and sufficient for identification.

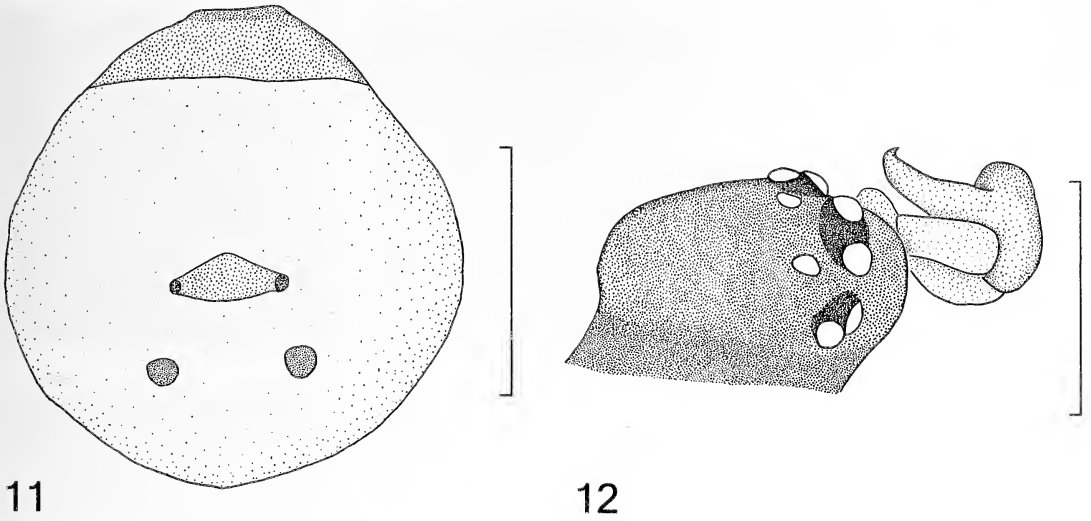
Distribution and habitat.—*Pararchaea corticola* is known only from the Queen's Domain, Hobart, Tasmania. Hickman (1969) recorded that the types were collected from under the loose bark of eucalypts.

Remarks.—I conducted field work at the Queen's Domain in January and February 2002, but found no evidence of this or any other *Pararchaea* species (despite targeted collecting). The forest was mainly dominated





Figures 9–10.—*Pararchaea bryophila*, male: 9. Left pedipalp, retro-ventral view, showing ornate distal plate and distinctive paracymbium; 10. Carapace, dorso-lateral view, showing medial indentation. Scale bar = 0.5 mm.



Figures 11–12.—*Pararchaea* species: 11. *P. saxicola*, holotype male abdomen, antero-dorsal view, showing small dorsal scute; 12. *P. corticola*, holotype male carapace and pedipalp, dorso-lateral view, showing retrolateral lobe-like extension at base of paracymbium. Scale bars = 0.5 mm.

by *Eucalyptus* trees and extensive grassland, and signs of a recent and widespread fire were apparent.

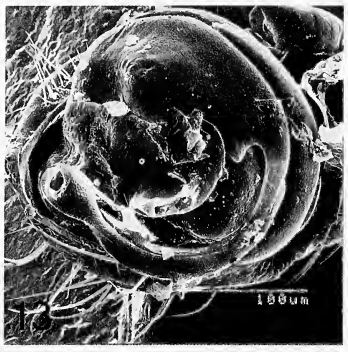
Pararchaea hickmani new species
(Figs. 3, 13–17)

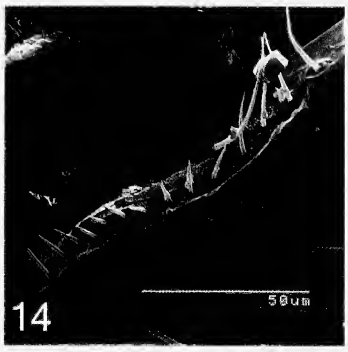
Type material.—Holotype male, Strathgordon, Tasmania, Australia, 42°46′S, 146°03′E, 17 January 2002, sifted from moss in forested valley overlooking inbound highway, M. Rix (AMS KS 82657). Allotype female, end of Basils Rd, West Downs via Ridgely, Tasmania, Australia, 42°20′S, 145°39′E, 1 December 1978, S737, map/grid reference 8015–853229, litter, D. DeLittle (AMS KS 82658).

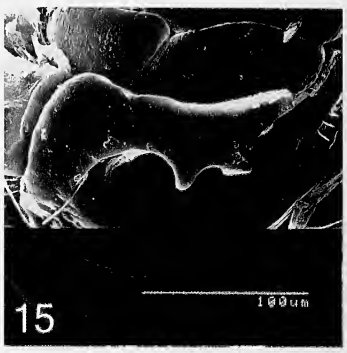
Other material examined.—AUSTRALIA: *Tasmania*: 1 ♀, Waterhouse Point (QVM 13: 46); 1 ♀, same data (QVM 13: 3244); 1 ♀, same data (QVM 13: 3212); 1 ♂, same data (QVM 13: 46); 1 ♀, same data (QM S16727); 1 ♂, Gordon River Road near Maydena (QM S60759); 1 ♂, 1 ♀, Mount Barrow (AMS KS 54299); 2 ♂, Punchbowl Reserve, Launceston (AMS KS 28719); 2 ♂, McPartlan Pass (QM S60758); 1 ♂, same data (QM S60760); 1 ♂, same data (QM S60761).

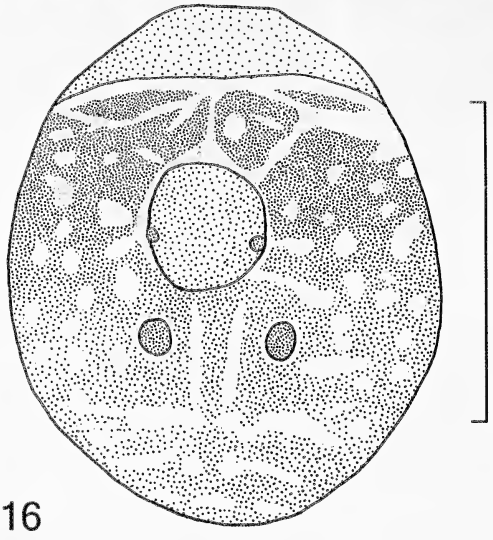
Diagnosis.—Female *P. hickmani* can be distinguished from all other known Tasmanian congeners by the 'marbled' abdominal coloration (in life), and the shape of the receptacula (the latter without distinct, 'nose-like' inward lobes; Fig. 3). Males can be distinguished from all other known Tasmanian congeners by the 'marbled' abdominal coloration (in life), and the small, circular dorsal scute (Fig. 16).

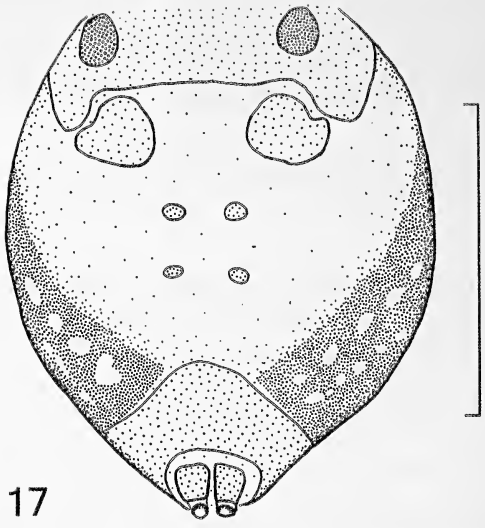
Description.—*Male (holotype AMS KS 82657):* Carapace 0.68 long, 0.45 wide. Abdomen 0.85 long, 0.63 wide. Total length 1.53. Color: carapace mustard-yellow. Abdomen pale cream, with light brown marbled patterning dorsally. Legs uniform pale cream. Carapace: in lateral view rhomboidal; dorsal surface of pars cephalica sloping almost linearly down to AME from posterior margin. Chelicerae: stridulatory ridges present on outer surface. Dentition: PTA 5, PTB 2, PTC 3 (10). Abdomen (Figs. 16–17): circular petiolar sclerite extending dorsally and ventrally (forming anterior sclerite); extending ventrally to cover entire epigastric region; extending dorsally to cover anterior face of abdomen. Post-epigastric region separately sclerotized, with two rounded sclerites (extending to half distance of epigastric furrow to VSP1 from latter). Small, roughly circular dorsal scute anterior and posterior to DSP1. Spinnerets encircled by sclerotized cuticle, extending ventrally up to length of VSQ from latter. Ventral internal sclerotic invaginations visible laterally and posteriorly. Abdomen clothed with black hairs; absent on antero-lateral faces. Pedipalp (Figs. 13–15): paracymbium curved, distally widened, with three small distal ex-









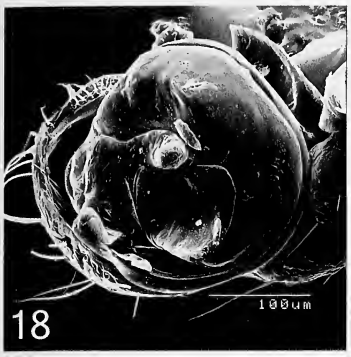


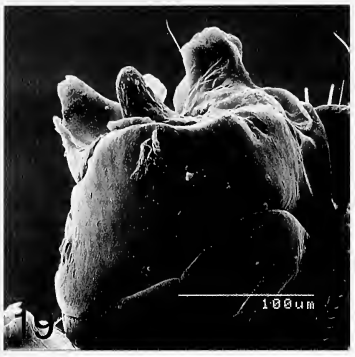
Figures 13–17.—*Pararchaea hickmani*, male: 13. Left pedipalp, ventral view, showing distally bifurcate embolus; 14. Left cymbium, retrolateral view, showing brush of hairs in groove; 15. Paracymbium of left pedipalp, retrolateral view, showing distinctive distal shape; 16. Abdomen, dorsal view, showing circular dorsal scute and 'marbled' coloration; 17. Abdomen, ventral view, showing separate post-epigastric sclerites. Scale bars = 0.5 mm.

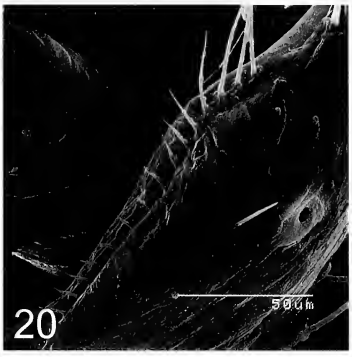
tensions. Distal plate complex, with median apophyses. Embolus distally bifurcate. Cymbium with brush of hairs in groove along retrolateral edge. Legs: femur I with dorsally curved row of 5 retrolateral denticles.

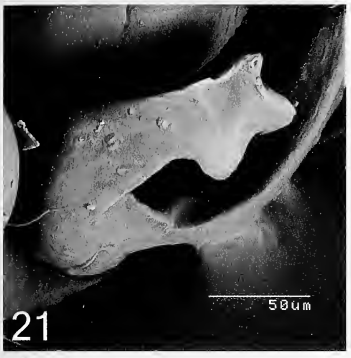
Female (allotype AMS KS 82658): Carapace 0.73 long, 0.48 wide. Abdomen 1.11 long, 0.82 wide. Total length 1.84. Color: carapace brownish-yellow. Abdomen mustard-yellow, with very light brown marbled patterning dorsally. Legs uniform mustard-yellow. Carapace: in lateral view rhomboidal; dorsal surface or pars cephalica weakly convex, sloping gently down to AME from posterior margin. Chelicerae: stridulatory ridges absent on outer surface. Dentition: PTA 5, PTB 3, PTC 3 (11). Abdomen: circular petiolar sclerite encircling petiole; not extending dorsally or ventrally. Epigyne surrounded by rectangular sclerite. Book lung covers plus triangular region posterior to each cover sclerotized. Two, small, square post-epigastric sclerites. Spinnerets encircled by sclerotized cuticle; cuticle medially constricted ventrally. Tracheal sclerite present. Ventral internal sclerotic invaginations visible laterally and posteriorly. Abdomen clothed with black hairs; absent on antero-lateral faces. Epigyne (QVM 13: 3244; Fig. 3): receptacula anteriorly widened, rounded; inward faces roughly straight, parallel. Legs: femur I with dorsally-curved row of 5 retrolateral denticles.

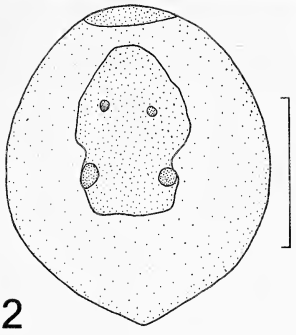
Distribution and habitat.—*Pararchaea hickmani* is widespread in Tasmania, where it

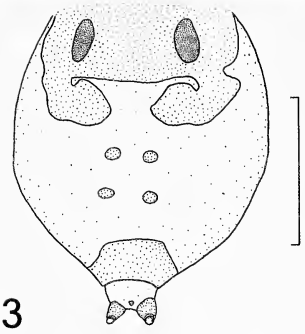












Figures 18–23.—*Pararchaea lulu*, male: 18. Left pedipalp, ventral view; 19. Left pedipalp, retro-ventral view, showing prominent median apophyses of distal plate; 20. Left cymbium, retrolateral view, showing brush of hairs in groove; 21. Paracymbium of left pedipalp, retrolateral view, showing distinctive distal 'star' shape; 22. Abdomen, dorsal view, showing longitudinally-elongate scute; 23. Abdomen, ventral view. Scale bars = 0.5 mm.

has been collected from moss (growing on the ground and on logs) and pitfall traps. The species is known from coastal and subalpine heathland habitats, and is the dominant *Pararchaea* species in some regions (pers. obser.).

Etymology.—The specific epithet is a patronym in honor of the late Vernon V. Hickman, for his substantial contribution to the study of Tasmanian Pararchaeidae.

Pararchaea lulu new species
(Figs. 4, 18–23)

Type material.—Holotype male, Warra Forest near Geeveston, Tasmania, Australia, 43°04′S, 146°43′E, 14 April 2000, ex. log decay, D. Bashford (QVM 13: 39992). Allotype female, same data as holotype (QVM 13: 39993).

Other material examined.—AUSTRALIA: *Tasmania*: 1 ♂, Warra Forest near Geeveston (QVM 13: 39994); 1 ♂, same data (QVM 13: 39995); 1 ♀, Pump House Point, Lake St Clair (QVM 13:23690); 1 ♀, 1 ♂, Lake Dobson Road, Mount Field National Park (QM S60757); 2 ♀, Arve Forest (AMS KS 28716); 1 ♀, Tarraleah (AMS KS 28724); 1 ♀, same data (AMS KS 28725); 1 ♀, Frodshams Pass (AMS KS 62695); 1 ♀, Mount Wellington (AMS KS 28722); 1 ♂, 1 ♀, same data (AMS KS 54298); 1 ♀, Fingal (AMS KS 28717); 1 ♀, Trevallyn (AMS KS 54296); 1 ♀, Fish River track to Walls of Jerusalem (AMS KS 54301); 1 ♂, southwest TAS (AMS KS 26475); 1 ♀, Strathgordon (AMS KS 28726).

Diagnosis.—Female *P. lulu* can be distinguished from all other known Tasmanian congeners by the pale abdominal coloration, and the shape of the receptacula (the latter with distinct, 'nose-like' inward lobes; Fig. 4). Males can be distinguished from all other known Tasmanian congeners by the pale abdominal coloration, the large, longitudinally-elongate dorsal scute (Fig. 22), and the distally 'star-shaped' paracymbium (Fig. 21).

Description.—*Male (holotype QVM 13:*

39992): Carapace 0.71 long, 0.53 wide. Abdomen 1.08 long, 0.82 wide. Total length 1.79. Color: carapace mustard-yellow. Abdomen pale yellow with mustard-yellow dorsal scute. Legs uniform light mustard-yellow. Carapace: in lateral view rhomboidal; dorsal surface of pars cephalica almost flat, except for slightly convex central region. Chelicerae: stridulatory ridges present on outer surface. Dentition: PTA 5, PTB 2, PTC 3 (10). Abdomen (Figs. 22–23): circular petiolar sclerite extending dorsally and ventrally (forming anterior sclerite); extending ventrally to cover entire epigastric and post-epigastric regions (extending to a little under half distance of epigastric furrow to VSP1 from latter); extending dorsally to cover anterior face of abdomen. Dorsal scute extending from behind posterior margin of anterior sclerite to half width of DSP2 from latter; widest posterior to DSP1, tapering anteriorly. Spinnerets encircled by sclerotized cuticle, extending ventrally up to length of VSQ from latter. Ventral internal sclerotic invaginations visible laterally and posteriorly. Abdomen clothed with black hairs; absent on antero-lateral faces. Pedipalp (Figs. 18–21): paracymbium curved, distally widened, with three distal extensions forming 'star-shape'. Distal plate complex, with prominent median apophyses. Embolus distally bifurcate. Cymbium with brush of hairs in groove along retrolateral edge. Legs: femur I with dorsally curved row of 4 retrolateral denticles.

Female (allotype QVM 13: 39993): Carapace 0.80 long, 0.55 wide. Abdomen 1.16 long, 0.94 wide. Total length 1.96. Color: carapace mustard-yellow. Abdomen pale cream. Legs uniform pale mustard-yellow. Carapace: in lateral view rhomboidal; dorsal surface of pars cephalica weakly convex, sloping gently down to AME from posterior margin. Chelicerae: stridulatory ridges absent on outer surface. Dentition: PTA 5, PTB 3, PTC 3 (11). Abdomen: circular petiolar sclerite encircling petiole; not extending dorsally or ventrally. Epigyne surrounded by rectangular sclerite. Book lung covers plus triangular extension posterior to each cover sclerotized. Two, small, square post-epigastric sclerites. Spinnerets encircled by sclerotized cuticle dorsally and ventrally; cuticle medially constricted ventrally. Tracheal sclerite present. Ventral internal sclerotic invaginations visible laterally and posteriorly. Abdomen clothed with black hairs; absent on antero-lateral faces. Epigyne (AMS KS 28716; Fig. 4): receptacula rounded, with prominent 'nose-like' inward lobes. Legs: femur I with dorsally curved row of 4 retrolateral denticles.

Distribution and habitat.—*Pararchaea lulu* is widespread in Tasmania, where specimens have been collected from moss and rotting logs.

Etymology.—The specific epithet is a patronym in honor of Lisa Boutin (nicknamed 'Lulu'), personal friend of the author, and collector of many recent pararchaeid and holarchaeid specimens. The name is to be treated as a noun in apposition.

Pararchaea ornata Hickman 1969
(Fig. 1)

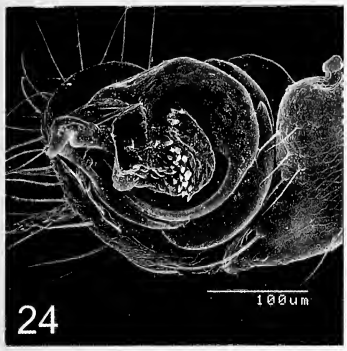
Pararchaea ornata Hickman 1969: 7, figs. 21–24.

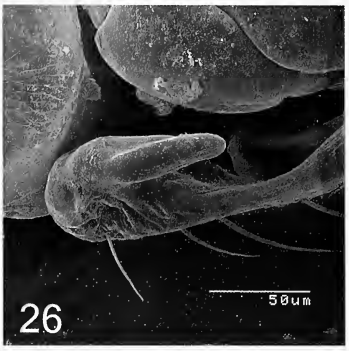
Type material.—Holotype female, The Queen's Domain, Hobart, Tasmania, Australia, 42°52'S, 147°19'E, 13 April 1968, shaking gorse (*Ulex europaeus*), V.V. Hickman (AMS KS 6638).

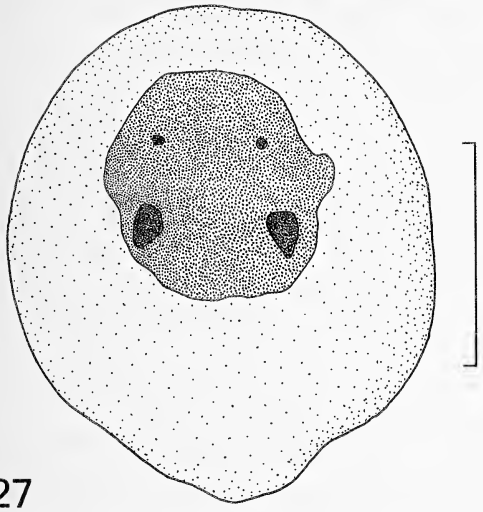
Other material examined.—AUSTRALIA: *Tasmania*: 1 ♂, 1 ♀, A3 roadside between Weldborough and Derby (QVM 13: 39996); 1 ♂, same data (QVM 13: 39997).

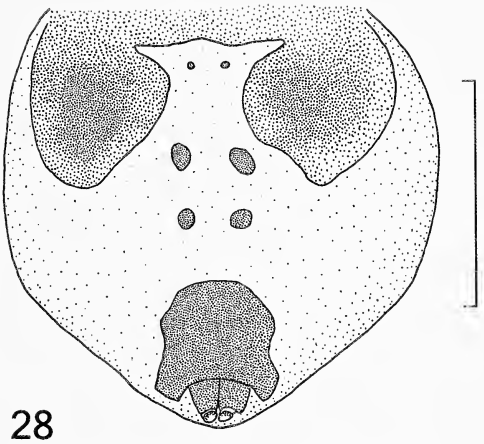
Diagnosis.—Female *P. ornata* can be distinguished from all other known Tasmanian congeners by the body coloration: the dorsal abdomen is pale yellowish, with dark brown posterior chevrons, a dark brown anterior cardiac stripe, and dark brown antero-lateral regions (Fig. 1). Males can also be distinguished from all other known Tasmanian congeners by the body coloration, which is similar to that of the female.

Description.—*Male (QVM 13: 39997):* Carapace 0.65 long, 0.48 wide. Abdomen 0.87 long, 0.71 wide. Total length 1.52. Color: pars cephalica and medial posterior region of pars thoracica mustard yellow; lateral pars thoracica dark brown. Abdomen pale yellow with dark brown cardiac stripe and five dark brown chevrons dorsally; antero-lateral regions also dark brown. Legs mustard yellow; metatarsi and tarsi banded brown proximally. Carapace: in lateral view rhomboidal; dorsal surface of pars cephalica weakly convex, sloping down to AME from posterior margin. Chelicerae: stridulatory ridges absent on outer surface.









Figures 24–28.—Male *Pararchaea robusta*: 24. Left pedipalp, ventral view; 25. Left pedipalp, retro-ventral view, showing prominent distal 'conductor'; 26. Paracymbium of left pedipalp, ventral view, showing simple, distally-rounded shape; 27. Abdomen, dorsal view; 28. Abdomen, ventral view, showing extensive post-epigastric sclerites. Scale bars = 0.5 mm.

Dentition: PTA 5, PTB 2, PTC 3 (10). Abdomen: circular petiolar sclerite extending dorsally and ventrally (forming anterior sclerite); extending ventrally to cover entire epigastric and post-epigastric regions (extending to two-thirds distance of epigastric furrow to VSP1 from latter); extending dorsally to cover anterior face of abdomen. Small, oval dorsal scute anterior and posterior to DSP1, fusing with anterior sclerite anteriorly. Spinnerets encircled by sclerotized cuticle, extending ventrally up to length of VSQ from latter. Ventral internal sclerotic invaginations visible laterally and posteriorly. Abdomen clothed with black hairs; absent on antero-lateral faces. Pedipalp: paracymbium pointed, sinuous, with inward hook. Legs: femur I with dorsally curved row of 4 retrolateral denticles.

Female (QVM 13: 39996): Epigyne: receptacula laterally rectangular, with distinctive 'nose-like' inward lobes.

Distribution and habitat.—*Pararchaea ornata* is known only from southern and north-eastern Tasmania. Hickman (1969) recorded that the holotype female was collected by shaking gorse (*Ulex europaeus*, Fabaceae). The species appears to be very rare.

Pararchaea robusta new species
(Figs. 5, 24–28)

Type material.—Holotype male, Frodshams Pass, Scotts Peak Road, 1.5 km west of Gordon River Road, Tasmania, Australia, 42°49′S, 146°13′E, 15 February 1990, *Nothofagus cunninghami* Sample 8, R. Coy, P. Lillywhite & A.L.Yen (VICM K-8796). Allotype

female, same data as holotype (VICM K-8797).

Other material examined.—AUSTRALIA: *Tasmania*: 1 ♀, Mount Wedge Track (QVM 13: 24033); 1 ♀, Liffey Falls (AMS KS 28713).

Diagnosis.—Female *P. robusta* can be distinguished from all other known Tasmanian congeners by the distinct, oval-shaped, posteriorly-convergent receptacula (Fig. 5). Males can be distinguished from all other known Tasmanian congeners by the extensive post-epigastric sclerites (Fig. 28).

Description.—*Male (holotype VICM K-8796):* Carapace 0.75 long, 0.50 wide. Abdomen 1.12 long, 0.93 wide. Total length 1.87. Color: carapace brown; pars thoracica darkest. Abdomen mustard-yellow, with dark brown dorsal scute. Legs mustard-yellow; femora, tibiae, metatarsi and tarsi banded brown proximally. Carapace: in lateral view rhomboidal; dorsal surface of pars cephalica weakly convex, sloping down to AME from posterior margin. Chelicerae: stridulatory ridges absent on outer surface. Dentition: PTA 6, PTB 3, PTC 3 (12). Abdomen (Figs. 27–28): circular petiolar sclerite extending dorsally and ventrally to cover entire epigastric and post-epigastric regions (extending to level between VSP1 and VSP2 behind epigastric furrow). Broadly oval dorsal scute extending from behind posterior margin of anterior sclerite to half length of DSQ behind latter; with lateral extension directly anterior to DS3. Spinnerets surrounded by sclerotized cuticle dorsally and ventrally, extending ventrally up to length of VSQ from latter. Ventral internal sclerotic invaginations visible laterally and posteriorly. Abdomen clothed with black hairs; absent on antero-lateral faces. Pedipalp (Figs. 24–26): paracymbium simple, curved, distally rounded. Distal plate ornately sclerotized, extending distally into prominent 'conductor'. Legs: femur I with dorsally curved row of 6 retrolateral denticles.

Female (allotype VICM K-8797): Carapace 0.94 long, 0.65 wide. Abdomen 1.33 long, 1.13 wide. Total length 2.27. Color: carapace brown; pars thoracica darkest. Abdomen mustard-yellow, with dark brown DSP2. Legs mustard-yellow; femora, tibiae, metatarsi and tarsi banded brown proximally. Carapace: in lateral view rhomboidal; dorsal surface of pars cephalica weakly convex, sloping down to AME from posterior margin. Chelicerae: stridulatory ridges absent on outer surface. Dentition: PTA 6, PTB 3, PTC 3 (12). Abdomen: circular petiolar sclerite encircling petiole; not extending dorsally or ventrally. Epigyne surrounded by rounded rectangular sclerite. Book lung covers plus triangular extension posterior to each cover sclerotized. Two, small, truncated-triangular post-epigastric sclerites. Spinnerets surrounded by sclerotized cuticle dorsally and ventrally; cuticle medially constricted ventrally. Tracheal sclerite present. Ventral internal sclerotic invaginations visible laterally and posteriorly. Abdomen clothed with black hairs; absent on antero-lateral faces. Epigyne (AMS KS 28713; Fig. 5): receptacula oval-shaped, posteriorly convergent. Legs: femur I with dorsally curved row of 6 retrolateral denticles.

Distribution and habitat.—*Pararchaea robusta* is known only from southern and central Tasmania.

Etymology.—The specific epithet refers to the robust appearance of this species.

Pararchaea saxicola Hickman 1969
(Figs. 2, 6, 11)

Pararchaea saxicola Hickman 1969: 5, figs. 16–20.

Type material.—Holotype male, The Queen's Domain, Hobart, Tasmania, Australia, 42°52′S, 147°19′E, 4 May 1938, *in copulo* on underside of loose stone on ground, V.V. Hickman (AMS KS 6639). Allotype female, same data as holotype (AMS KS 6640).

Other material examined.—AUSTRALIA: *Tasmania*: 1 ♀, The Queen's Domain, Hobart (AMS KS 54297).

Diagnosis.—Female *P. saxicola* can be distinguished from all other known Tasmanian congeners by the distinctive, large, 'comma-shaped' receptacula, broadly touching along their inward margins (Fig. 6). Males can be distinguished from all other known Tasmanian congeners by the very small, transversely-elongate dorsal scute (Fig. 11).

Description.—Male (holotype AMS KS 6640)*:* Pedipalp: bulb expanded. Paracymbium curved, with inner hook. Distal plate projecting over embolus; both interacting with paracymbium on retrolateral side.

Female (AMS KS 54297)*:* Epigyne (Fig. 6): receptacula large, 'comma-shaped', broadly touching along inward margins.

Distribution and habitat.—*Pararchaea saxicola* is known only from the Queen's Domain, Hobart, Tasmania, and was collected from under stones in May 1936.

Remarks.—I conducted field work at the Queen's Domain in January and February 2002, but found no evidence of this or any other *Pararchaea* species (despite targeted collecting). The forest was mainly dominated by *Eucalyptus* trees and extensive grassland, and signs of a recent and widespread fire were apparent.

Family Holarchaeidae Forster & Platnick

Holarchaeidae Forster & Platnick 1984: 71.

Type genus.—*Holarchaea* Forster, by original designation.

Diagnosis.—The Holarchaeidae can be distinguished from all other spider families by elongate chelicerae arising from a distinct but ventrally unsclerotized foramen, in combination with entelegyne female genitalia, an absence of peg teeth on the chelicerae and a swollen (anteriorly projecting) clypeus (see Forster & Platnick 1984). Holarchaeid spiders can also be recognized by having tarsi longer than metatarsi, widened female pedipalps distally, and spherical abdomens.

Distribution.—The Holarchaeidae are known only from Tasmania and New Zealand. Despite extensive surveying of Victorian *Nothofagus* (beech) forests (Graham Milledge, pers. comm.), holarchaeid spiders have not been found on the Australian mainland.

Remarks.—The Holarchaeidae are a morphologically and biogeographically distinct spider family, unlikely to be confused (upon close examination) with any other Araneae. New Zealand *Zearchaea* (Mecysmaucheniidae) appear superficially similar to *Holarchaea*, but with only two spinnerets, peg teeth, and a foramen completely surrounded by sclerotized cuticle, the former genus is easily distinguished.

Holarchaea Forster 1955

Holarchaea Forster 1955: 392; Forster & Platnick 1984: 76.

Type species.—*Archaea novaeseelandiae* Forster 1949, by original designation.

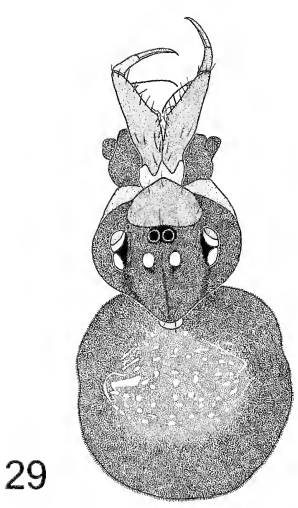
Diagnosis.—As for family.

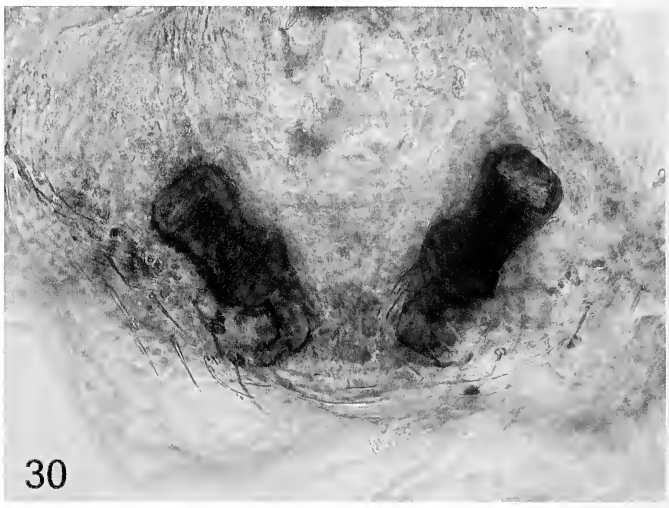
Generic description.—In part from Forster & Platnick 1984.

Cephalothorax: Carapace, when viewed laterally, anteriorly raised or triangular. Pars cephalica rising steeply from pars thoracica above level of coxa III. Lateral pars thoracica with furrow ventro-lateral to pars cephalica, dorsal pars thoracica slightly concave centrally. Viewed dorsally, carapace rounded; posterior margin of pars cephalica appearing demarcated from rest of carapace, extending to PLE. Carapace cuticle without tubercles, sometimes punctate. Eight eyes in two rows; laterals contiguous, pearly-white, widely separated from medians; AME smallest, circular, closely-spaced, dark-colored; PME oval, pearly-white, well separated. Carapace mainly devoid of hairs, except on postero-dorsal aspect of pars cephalica, clypeus and around eyes. Anterior margin of carapace encircling bases of chelicerae, with unsclerotized cuticle extending ventrally to form antero-ventrally-facing oval foramen. Clypeus large, swollen, projecting anteriorly and laterally around bases of chelicerae, connecting with sclerotized cuticle of anterior carapace ventro-laterally; longest medially (forming dorsal margin of foramen). Margin of pars thoracica smoothly curved, with separate, elongate sclerite above coxae III and IV on each side. Sternum longer than wide, posteriorly obtuse; cuticle lightly punctate. Maxillae directed across labium, not meeting in middle; serrula a single row of teeth. Labium triangular, wider than long; strongly rebordered.

Chelicerae: Paturon (Figs. 34 & 35) relatively long, elongate, constricted proximally; cuticle finely reticulated. Fang (Figs. 34–36) long, distally curved, usually hooked at tip, with raised, finely serrated prolateral edge (Fig. 36); divided at one third of length from base by transverse groove; without poison gland opening. Two or three true slender teeth on prolateral margin of paturon (Fig. 35); peg teeth absent. Pored cheliceral gland mound situated near tip of non-extended fang; retro-laterally-adjacent to proximal tooth. Hairs sparse; several filiform.

Legs and female pedipalp: Legs (longest to shortest: 1, 4, 2, 3) relatively long, slender, cuticle finely reticulated, clothed with slender smooth or weakly serrate hairs; no spines or scopulae. Single trichobothrium on metatarsi, 2 or 3 on tibiae; bothria well developed with smooth posterior hood. Tarsi longer than metatarsi, with three smooth claws; tarsi I and





Figures 29–30.—*Holarchaea globosa*: 29. Male cephalothorax and abdomen, antero-dorsal view; 30. Cleared female receptacula, dorsal view, showing bilobed morphology of each receptaculum.

II with reduced claws. Distal quarter of tarsi I and II more slender than proximal three-quarters; often with group of modified, strongly serrate hairs raised on low mounds, surrounding discoid organs of unknown function. Tarsal organ capsulate. Tibia and tarsus of female pedipalp shortened, widened, partially fused; with brush of long hairs ventrally; without claw.

Abdomen: Abdomen spherical or globose. Cuticle thin, without scutes or surface swellings; clothed with short hairs. Female epigyne a single slit-like opening, shortly anterior to epigastric furrow; lightly sclerotized, obscured by posterior of sternum in live animals and many specimens. Anterior respiratory openings lightly sclerotized. Six spinnerets; ALS largest, PMS smallest. Posterior tracheal spiracle absent. Colulus linguiform, with two posteriorly projecting hairs.

Male genitalia: Pedipalp (Figs. 31–33) with coiled embolus encircling bulb two or three times. Ventral surface of bulb relatively smooth (Fig. 32), without prominent apophyses. Cymbium spoon-shaped, with or without spine-like proximal retrolateral apophysis (Fig. 33). Patella and tibia variably-shaped, with spur-like processes distally (Fig. 33).

Female genitalia: Epigyne with single slit-like opening leading to pair of unilobed or bilobed receptacula (Fig. 30); each receptaculum with short, proximal, spur-like fertilization duct leading into bursal cavity.

Included species.—*Holarchaea globosa* (Hickman 1981), *H. novaeseelandiae* (Forster 1949).

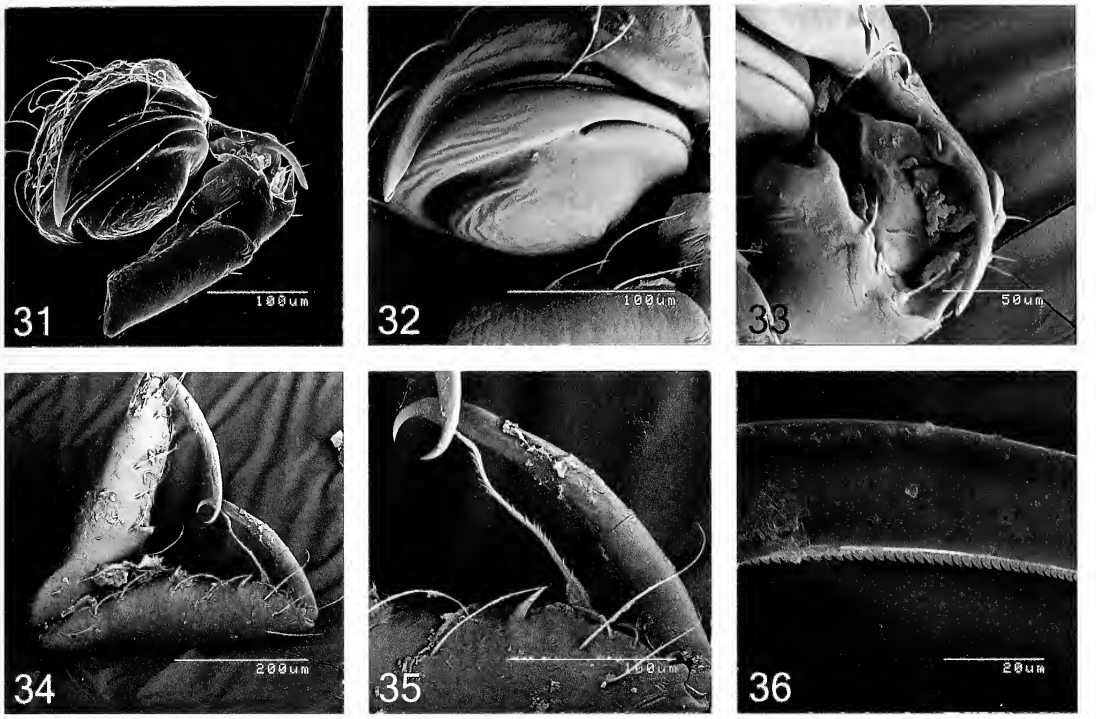
Holarchaea globosa (Hickman 1981)
(Figs. 29–36)

Zearchaea globosa Hickman 1981: 47, figs. 1–5.
Holarchaea globosa (Hickman): Forster & Platnick 1984: 76.

Type material.—Holotype female, Strathgordon, Tasmania, Australia, 42°46′S, 146°03′E, 25 April 1978, from moss, V.V. Hickman (AMS KS 6987).

Other material examined.—AUSTRALIA: *Tasmania*: 1 ♂, 1 ♀, Hogarth Falls Walk, People's Park, Strahan (QM S60756); 1 ♀, Main Cave (MU201–13v E-Tw-Tr), Montagu (QVM 13:12671); 1 ♀, same data (AMS KS 29515); 5 ♀, 2 ♂, Andrew River Caves, Western Heritage Area (AMS KS 21290); 1 ♀, Cuckoo Falls Walk, southeast of Scottsdale (QM S60755).

Diagnosis.—Male and female *H. globosa* can be distinguished from all other known congeners by the triangular shape of the carapace in lateral view (with highest point of pars cephalica separated from PME by distance greater than medial length of clypeus). Other autapomorphies include the single long, serrate, moveable hair near the base of each fang (Fig. 35), fangs with length greater than half length of paturon (Fig. 34), fangs without hooked tips (Fig. 35), a posteriorly-directed,



Figures 31–36.—*Holarchaea globosa*, pedipalp and chelicerae: 31–33, Male left pedipalp; 31. Distal segments, retrolateral view; 32. Bulb and cymbium, retro-ventral view, showing pointed distal process of cymbium; 33. Cymbium, tibia and patella, retrolateral view, showing proximal, posteriorly directed, spine-like process of cymbium and complex tibia and patella. 34–36. Female chelicerae: 34. Chelicerae, frontal view, showing relative lengths of paturon and fang; 35. Fang, distal tooth and moveable hair of right chelicera, frontal view, showing distally curved fangs and morphology of serrate moveable hair; 36. Fang, showing strongly serrated prolateral edge.

spine-like proximal apophysis on the male palpal cymbium (Fig. 33) and bilobed, distally and proximally spherical female receptacula (Fig. 30).

Without a cladistic analysis of the entire Australasian holarchaeid fauna, it is unclear whether the above autapomorphies are indicative of a highly derived species of *Holarchaea* (congeneric with the New Zealand species *H. novaeseelandiae*), or of a monotypic Australian genus, sister to the former.

Description.—*Male (QM S60756):* Carapace 0.45 long, 0.40 wide. Abdomen 0.60 long, 0.55 wide. Total length 1.05. Color: carapace dark brown. Abdomen dark brown with lighter dotted striations anteriorly and anterolaterally. Legs uniform brown. Body and legs shiny black in life. Carapace (Fig. 29): in lateral view triangular; highest point of pars cephalica separated from PME by distance greater than medial length of clypeus. Clypeus swollen; triangular in dorsal view. Chelicerae: elongate, constricted proximally, with single long, serrate, proximally-widened/flattened moveable hair projecting from near base of fang. Fang greater than half length of paturon; tip curved but not hooked; without poison gland opening. Dentition: 2 prolateral (true) teeth, widely spaced. Abdomen (Fig. 29): spherical, without surface sclerotization. Pedipalp (Figs. 31–33): patella large, wedge-shaped, with distal spurs. Tibia complex, twisted. Cymbium spoon-shaped, with prominent, posteriorly directed, spine-like apophysis proximally; retro-distally with broad, pointed apophysis. Ventral surface of bulb relatively smooth. Embolus coiled.

Female (QM S60756): Epigyne (Fig. 30): receptacula elongate, bilobed.

Distribution.—*Holarchaea globosa* specimens are known from south-west, west, north-west, south-central and north-east Tasmania.

Remarks.—Adult specimens of *Holarchaea globosa* have been collected at various

months of the year, including January, February, April, May and October.

General biology.—Very little is known about the biology of *H. globosa*. From the relatively few collection details available, it would appear that the species is restricted to wet and consistently humid habitats. Most specimens have been found on ferns or within moss and leaf litter in temperate rainforest (although several specimens have also been collected from caves: Main Cave near Montagu, Andrews River Caves and Cardia Cave near Acheron River, see Eberhard et al. 1991). Of these, the majority have not been observed alive (e.g., they were collected using tullgren extractions or pyrethrum fogging). However, I collected four *H. globosa* alive in January 2002: two from Hogarth Falls near Strahan (1 male & 1 female) and two from Cuckoo Falls near Scottsdale (1 juvenile & 1 female). All four specimens were collected from among the leaves of the 'hard water fern' (*Blechnum wattsii*, Blechnaceae), an abundant, low-growing species within many Tasmanian rainforests (Garrett 1996). The former two were found close to midnight, during persistent rain, with the male seen hanging from a single line of silk between the fern leaves. The female was swept from vegetation nearby. The Cuckoo Falls female was beaten from ferns in tall beech (*Nothofagus*) and tree fern forest during overcast and humid conditions, whilst the juvenile was collected in the same manner, close to the waterfall. Interestingly, a male and female were also collected by Lisa Boutin (QVM) at Hogarth Falls four years earlier, again during persistent rain. The diet of *H. globosa* is unknown, although of the organisms beaten from the *Blechnum* and tree ferns, oribatid mites, collembola and other spiders dominated.

Observations of live specimens.—Live *H. globosa* were maintained alive in captivity from 27 January until 11 February, 2002.

The *H. globosa* specimens I collected (see General Biology, above) were all shiny black in life (this appearance was rapidly lost after ethanol preservation), and superficially not unlike small theridiid spiders. Both sexes were agile when walking along a line of silk, but spent most of their time in captivity hanging or clinging upside-down. When lowered onto a horizontal surface the spiders would walk around until they found an object to assail, then proceed upwards to find a suitable position for resuming an upside-down pose. While walking the spiders would regularly wave their first two pairs of legs around in the air, and when at rest would occasionally do the same (with leg I). In the upside-down resting position the legs were held close against the carapace and abdomen, and the elongate chelicerae were held vertically and flat against the anterior cephalothorax and endites (at an angle to each other, to form a triangle in anterior view). While the chelicerae of many holarchaeid specimens (in ethanol) point at an angle to the cephalothorax (due to relaxation of the cheliceral muscles during preservation), those of the live spiders were not seen to extend to such a degree, and the only cheliceral movement observed was of strictly diaxial form (when the spiders 'cleaned' their legs with their mouthparts).

INTERRELATIONSHIPS OF THE AUSTRALIAN TAXA

Species-group relationships are hypothesized and outlined below for the eight described Australian pararchaeid species. Without a full revision and cladistic analysis of the family, it is unclear whether the groups as here delimited represent separate monophyletic genera, or merely clusters of similar species united by substantial homoplasy. However, multiple somatic and correlated genitalic similarities clearly exist between groups of Australian species of *Pararchaea*, and the majority of species examined by the author, including those currently undescribed from the Australian mainland, can be attributed to one of the four putatively monophyletic clades as here diagnosed.

Pararchaea saxicola species group

Diagnosis.—United by: femur of leg I with proximal retrolateral denticles; male abdomen with small to very small dorsal scute (separate or fused to anterior sclerite), not surrounding or extending posterior to level of DSP2; male pedipalp with relatively short, inwardly hooked paracymbium, and without brush of hairs in groove along retrolateral edge of cymbium.

Distribution.—Known from north-eastern Queensland, south-eastern Queensland, north-eastern New South Wales, Tasmania and south-western Western Australia.

Included species.—*Pararchaea ornata* Hickman, *P. saxicola* Hickman, and several unnamed species.

Pararchaea lulu species group

Diagnosis.—United by: femur of leg I with proximal retrolateral denticles; male abdomen with small to medium-sized, pale dorsal scute (often longitudinally elongate), usually extending posterior to level of DSP2; male pedipalp with brush of hairs in groove along retrolateral edge of cymbium and distally expanded, bifurcate embolus.

Distribution.—Known from north-eastern, middle-eastern and south-eastern Queensland, eastern New South Wales, Victoria and Tasmania.

Included species.—*Pararchaea lulu* new species, *P. hickmani* new species and several unnamed species.

Pararchaea corticola species group

Diagnosis.—United by: femur of leg I with proximal retrolateral denticles; male abdomen with large, broad, dark brown dorsal scute, surrounding and extending posterior to level of DSP2; male pedipalp with prominent distal extension of distal plate into pointed 'conductor', without brush of hairs in groove along retrolateral edge of cymbium.

Distribution.—Known from south-eastern Queensland, eastern New South Wales, Victoria and Tasmania.

Included species.—*Pararchaea binnaburra* Forster, *P. corticola* Hickman, *P. robusta* new species and several unnamed species.

Pararchaea bryophila species group

Diagnosis.—United by: femur of leg I without proximal retrolateral denticles; postero-dorsal aspect of male pars-cephalica with medial indentation; male anterior tarsus distinctly swollen proximally; male abdomen with large, broad dorsal scute, extending posterior to level of DSP2; male pedipalp without brush of hairs in groove along retrolateral edge of cymbium; female receptacula together forming distinctive, posteriorly convergent 'V-shape', with 'nose-like' inward lobes.

Distribution.—Known from south-eastern Queensland, eastern New South Wales, Victoria and Tasmania.

Included species.—*Pararchaea bryophila* Hickman, and several unnamed species.

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RELATIONSHIP BETWEEN ESCAPE SPEED AND FLIGHT DISTANCE IN A WOLF SPIDER, *HOGNA CAROLINENSIS* (WALCKENAER 1805)

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ABSTRACT. The relationship between running speed and flight distance is an important one in terms of escape from predators, especially in species that may have multiple defensive strategies. In the wolf spider *Hogna carolinensis*, one important antipredator mechanism is flight. We examined the relationship between sprint speed and flight distance in wolf spiders by measuring sprint speed on a running track and, in a separate set of experiments with the same individual spiders, measured the distance at which they fled from an advancing model predator. Sprint speed was not significantly correlated with mass, size, or sex of the spiders. Sprint speed was positively correlated with flight distance. This correlation may be the result of a trade-off between two competing modes of antipredator mechanisms: escape and crypsis. In individuals with higher sprint speeds, escape may be the more advantageous option. Slower individuals may have a greater chance of surviving an encounter with a predator simply by remaining still and relying on crypsis.

Keywords: Antipredator strategy, risk, flee, sprint speed

Behavior patterns associated with predator escape and avoidance are important to individual survival. These result in strong selective pressure favoring individuals that successfully avoid or escape from predators. When an animal is approached by a potential predator, it must evaluate the level of predation risk, and utilize the appropriate antipredator mechanism to neutralize the risk. The distance from an approaching predator at which an animal chooses to flee has been referred to as "flight distance" (e.g. Fernández-Juricic et al. 2002), "flight initiation distance" (e.g. Bonenfant & Kramer 1996), "approach distance" (e.g. Martin & Lopez 1999), and "flush distance" (e.g. Fernández-Juricic et al. 2001). The latter two of these imply the perspective of the predator. Since we will be discussing the issue from the perspective of the prey, "flight distance" seems the most appropriate and concise terminology.

Ydenberg & Dill (1986) discussed in detail the economics of escape from predators. They suggested a cost-benefit model of flight distance, incorporating the costs and benefits of continuing a particular behavior (such as foraging) relative to the costs and benefits of fleeing. A concept critical to the predictions made by Ydenberg & Dill's (1986) model is that "response" does not necessarily equal "detection," in that it can often be difficult to assess whether or not the potential prey has detected a predator. In some cases, an individual may ignore an approaching predator until it becomes necessary to initiate flight. In other cases, certain "alert behaviors" may occur that precede a flight decision. The Ydenberg-Dill model generally predicts that individuals should delay flight until the costs associated with staying (e.g., increased predation risk) exceed the benefits associated with staying (e.g., time spent searching for food or mates).

Several studies have examined the relationship between flight distance and running ability. Rand (1964) found that body temperature affected the distance at which *Anolis* lizards fled from approaching predators, attributing differences in escape distances among individuals to lower body temperatures which reduced sprint speeds. Cooler individuals tended to flee at greater distances because lower body temperatures result in greater risk of capture. Heatwole (1968) suggested that crypsis might also play a role in flight distances. Cryptic species of *Anolis* may decrease their risk of capture by remaining motionless and fleeing

at shorter distances than less cryptic species. Species that rely on crypsis may not flee from an approaching predator until detection by the predator is certain.

Schwarzkopf & Shine (1992) suggested that "vulnerability" (risk of capture) of prey should be evaluated in terms of the probability of being detected by a predator. They found that gravid female water skinks, *Eulamprus tympanum*, exhibited decreased running ability and shorter flight distances relative to nongravid females. They suggested that gravid females switched antipredator tactics from escape to crypsis because of the decrease in running speed. They interpreted these results as evidence that escape speed may not always be the most important element involved in determining when to flee. Formanowicz et al. (1990) investigated similar effects in the lizard *Scincella lateralis* with differences in sprint speed related to tail autotomy. Skinks with autotomized tails were found to exhibit slower running speeds and relatively shorter flight distances. They suggested that individuals that had lost their tails switched to a cryptic antipredator strategy to compensate for reduction in sprint speed.

In this study, we examined the relationship between running speed and flight distance in the wolf spider *Hogna carolinensis* (Walckenaer 1805). *Hogna carolinensis* is a large, burrowing wolf spider that is active on the surface of the ground from dusk until dawn and is distributed from southernmost Maine and Ontario throughout the southeastern U.S. and west to Baja California (Dondale & Redner 1990). Very little has been published concerning the life history of this species. Individuals of *Hogna carolinensis* construct a burrow with a turret of sticks and grass surrounding the mouth of the burrow. Or, in some cases, these spiders may inhabit a deserted rodent burrow (Shook 1978). The depth of the burrow likely varies between geographical regions and possibly with the substrate. In west Texas, where this study was conducted, I have found burrows as deep as 25 cm (pers. obs.). Likely predators include lizards, centipedes (pers. obs.), scorpions, coyotes, owls and various predacious insects (Shook 1978). If a burrow is near, individuals will retreat to a burrow when disturbed (Kuenzler 1958); however, if a burrow is not near, the animal will usually flee a meter or so, and then remain motionless (pers. obs.).

We examined the relationship between body size and running speed in male and female *H. carolinensis*, testing the hypothesis that larger individuals were faster. Since there is a sexual dimorphism in body size in this species, we also predicted that females and males should differ in running speed. Using the same spiders, we examined the distance at which they fled from an approaching model predator. We used the data collected on running speed and flight distance to test the following hypothesis based on Ydenberg & Dill's (1986) model: faster individuals would be expected to flee at shorter distances from the predator.

METHODS

Hogna carolinensis (n = 77; 44 males, 33 females) used in this study were collected on 26 March and 11 April, 1997 at the Texas Nature Conservancy's Independence Creek Preserve, approximately 37 km south of Sheffield, Terrell County, Texas, on the northeastern edge of the Chihuahuan desert. Voucher specimens have been deposited at the Denver Museum of Nature & Science. Most spiders were collected at night by using headlamps to produce eyeshine; a few were collected by turning rocks during the day. Spiders were not found to be active during the day. Females were often found near the mouth of a burrow, and sometimes removed from a burrow. In almost every case, females were found within a meter of the burrow. Males, however, were only occasionally found near a burrow but never in a burrow. Spiders were housed individually, in clear plastic containers (18.5 × 7.5 × 9 cm) with a sand substrate (approx. 1 cm deep). Each spider was fed one adult cricket/week, and water was available ad libitum. Temperatures in the housing and testing area ranged from 25–26 °C.

Escape Speed.—Spider escape speeds were measured on a wooden track 9 cm wide and 2 m long, with sheet-metal side walls approximately 21 cm high. All trials were conducted during daylight hours. A start box was separated from the track by a removable metal divider (21 × 9 cm). A spider was placed in the start box, allowed to acclimate for 15 minutes, the divider was raised, and the spider was prodded on the posterior end of the abdomen

with a fiberglass rod until it ran. Using a stopwatch, we recorded the time that the spider crossed each 50 cm segment of track. Each spider was run twice with 24 hours between trials, after which time its mass was recorded. Spider cephalothorax lengths were measured at the end of the study with a caliper.

The fastest 50 cm speed (cm/s) for each spider was used for statistical analyses. T-tests were used to determine whether mass, cephalothorax length and speed differed between the sexes. Normality was evaluated using Shapiro-Wilk's W, and none of the groups violated this assumption at 0.05 level. Pearson correlation coefficients were used to examine relationships between speed and mass, speed and cephalothorax length, and mass and cephalothorax length.

Flight distances.—The distances at which spiders fled from an approaching model predator were recorded using a wooden runway apparatus 2.7 m long, and 28 cm wide with black plastic walls approximately 48 cm high. The spider chamber (32 × 28 × 51 cm) was located at one end of the runway, and separated from the runway by a glass divider. The walls of the spider chamber were sheet metal with two observation holes (0.5 cm diameter) that allowed the spider to be viewed with minimal disturbance. The floor of the spider chamber had a sand substrate 11 cm deep. To minimize vibratory cues, the runway and the spider chamber were separated from the counter top by 5.5 cm of foam rubber, and separated from each other by a space of 2 cm. A 15 cm tall green plastic lizard was used as a model predator (meant to represent a novel predator rather than a particular known predator) to elicit escape behavior. Each spider was placed in the spider chamber for 10 min. to acclimate. The model predator was concealed by a black plastic curtain at the end of the runway, opposite the spider chamber. After 10 min., the model predator was pulled toward the spider using a length of fishing line connected to a spool that was turned by a small motor at a speed of approximately 33.9 cm/s (mean = 1.4747 ± 0.0922 [seconds per 50 cm segment]). We ran a set of 10 test trials where we measured four 50 cm segments of track to test for consistency of speed of the model predator. Repeated-measures ANOVA (using trial as the repeated measure) showed no significant effect ($F_{9,27} = 0.4963$; $P = 0.8640$) indicating that the speed of the model predator from trial to trial was not significantly different. Another set of trials was run using only the motor without the model predator to rule out the possibility of cues from the sound and vibration of the motor. In these trials, none of the spiders responded to the activation of the motor ($n = 10$). The response of the spider to the approaching model predator was viewed through the observation holes in the wall of the spider chamber. Escape was operationally defined as a spider turning and running in the opposite direction from the model predator. When the spider exhibited an escape response, the motor was stopped and the distance was measured from the front end of the model to the original position of the spider. Spiders were run only once, unless no response occurred, in which case they were given a second trial. Flight distances were determined for thirty-eight of the individuals (19 males, 19 females) whose escape speeds had been measured.

Flight distances were transformed using the natural log to alleviate normality issues. Pearson correlation coefficients were calculated to examine the relationships between flight distance and spider size (mass & cephalothorax length) and sprint speed (as measured above). Discrepancies in sample size between tests resulted from specimen mortality and unresponsiveness of some individuals. All statistical tests were carried out using SPSS 11.0.2.

RESULTS

Escape Speed.—This species shows some degree of sexual size dimorphism (cephalothorax length: females, $n = 43$, mean ± SE = 12.92 ± 1.09 mm; males, $n = 33$, mean ± SE = 11.94 ± 0.74mm). Female *H. carolinensis* are significantly larger than males (mass, $t_{52} = 3.946$, $P < 0.001$ two-tailed; cephalothorax length, $t_{72.947} = 4.641$, $P < 0.001$ two-tailed [unequal variances]). Mass and cephalothorax length were significantly correlated (Pearson's $r = 0.470$, $P < 0.001$). However, when correlations were examined separately for the two sexes, this relationship only held true for the males ($r = 0.439$, $P = 0.017$, males; $r = 0.209$, $P = 0.326$ females). Although males and females differed in both measures of size, their sprint speeds were not significantly different ($t_{55} = 1.439$, $P = 0.156$, two-tailed). Neither mass nor cephalothorax

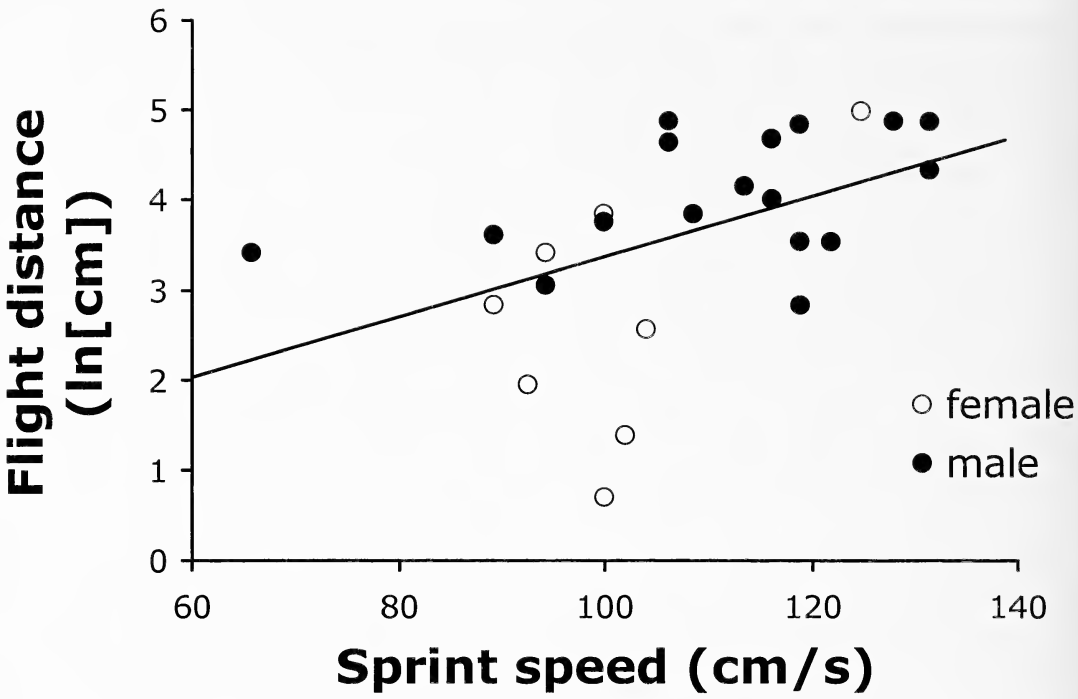

Figure 1.—Scatterplot of the natural log of flight distances and sprint speeds (r^2 = 0.241, P = 0.013).

length was significantly correlated with fastest sprint speed (Pearson's r = −0.145, P = 0.296, n = 54; r = 0.077, P = 0.571, n = 56, respectively).

Flight distance.—There was no significant correlation between spider size and log flight distance (mass, Pearson's r = 0.024, P = 0.916, n = 22; cephalothorax, r = −0.314, P = 0.055, n = 38). However, males tended to flee from the model predator at greater distances than females (t_{37} = 2.663, P = 0.011, *two-tailed*). Furthermore, there was a positive correlation between fastest sprint speed and log flight distance (Pearson's r = 0.491, P = 0.013, n = 25, see Figure 1).

DISCUSSION

The results of our study indicate that sprint speeds and flight distances of *H. carolinensis* are not affected by spider size. There were no significant differences in speed between males and females and no significant correlation between sprint speed and either measure of size (mass or cephalothorax length). Although size does not affect sprint speed or flight distance, sex appears to affect the decision to flee. Males fled from the model predator at greater distances than females.

Differences in flight distances for males and females may be the result of different cost-benefit relationships for males and females. Males and females may have very different lifestyles that require different considerations. Shook (1978) suggested that females might tend to stray farther from the burrow than males. If this is true, they may have a different escape strategy. For spiders associated with burrows, escape consists of only a short sprint to a burrow. However, for an individual that is not near its burrow, escape may involve a longer sprint, as well as an assessment of available shelter. To date, we have not been successful in getting this species to occupy burrows in the lab. Although females will occasionally inhabit a man-made burrow, none of our spiders have excavated their own burrows in the lab. In the field, males were rarely found near a burrow. It is possible that male *H. carolinensis* are not usually associated with a burrow and, therefore, are more reliant upon running to escape a predator. It would be interesting to determine whether flight distance is related to distance from the burrow in this species as has been shown in other organisms (squirrels, Dill & Houtman 1989; Cichlid fish,

Dill 1990; woodchucks, Bonenfant & Kramer 1996; and skinks, Cooper 1997).

Sexual size dimorphism is common in spiders. Although not as exaggerated in wandering spiders as it is in web-builders, size dimorphism is still present. In wolf spiders, females may have longer cephalothoraxes, larger chelicerae, and larger abdomens than males (Walker & Rypstra 2001). The different body shape of males and females may result in different values for costs and benefits used in decision-making. The lack of a correlation between mass and cephalothorax length among females reflects the overall difference in body shape between males and females. The stouter build of the female in this species results in the size of the abdomen contributing more to overall mass than in males. Males have a smaller abdomen relative to cephalothorax length. As a result, males may possess lower energy stores, therefore placing a higher value on foraging. Females are generally considered to be more effective foragers than males, since they often consume more prey items (e.g. Walker & Rypstra 2001). It is, however, possible that males consume less due to their smaller size, but are more reliant on regularity of foraging success than females. In this case, a male that has not fed recently may be willing to risk predation in order to continue foraging. However, a male that has recently fed may flee when an approaching predator is farther away. It would be interesting to determine if feeding regime or the time since last feeding has an effect on flight distance and if that effect is different for males and females.

There was a positive correlation between sprint speed and flight distance. Spiders that were faster fled at greater distances from the approaching model predator while slower spiders waited until the model predator was closer before fleeing. This relationship between sprint speed and flight distance may seem counter-intuitive. The cost-benefit model of Ydenberg & Dill (1986) predicted that faster individuals should wait until the predator was closer before attempting to escape. When the predator is still relatively far away, the cost of flight (lost foraging time) would be higher than the risk of predation (risk of capture), resulting in an inverse relationship between maximum sprint speed and flight distance. According to the model, faster individuals are more likely to continue foraging, since the risk of capture for any given distance is less for a faster individual than for a slower individual.

In the present study, the individuals were not performing any specific task. We therefore need to consider what costs may be associated with flight and what benefits may be associated with staying. For spiders, the energy expended during escape can be costly (Prestwich 1988). Therefore, in cases where the risk of capture is low, it may not be worth the effort for the individual to attempt to escape. This cost might be higher for females, since they are larger than males and may have to expend more energy when running.

Another, perhaps more important cost of flight in some species involves cryptic antipredator mechanisms. In cryptic species, flight may actually increase the risk of capture (Heatwole 1968; Regalado 1998; Cuadrado et al. 2001). As a predator approaches a cryptic individual, the individual must decide whether it has been detected, making it necessary to flee. If, however, the individual flees before the predator has detected it, the individual may draw attention to itself and increase its risk of capture. The individual may also attract other potential predators. In this type of situation, the cost of flight is related to the probability of detection by the potential predator. This is a function of the perceptual fields of both the predator and prey species. If the predator has a larger perceptual field than the prey, the prey would benefit by fleeing while the potential predator is still relatively far away. When the predator has a smaller perceptual field than the prey, the prey would benefit by waiting to flee until the predator is closer, and the probability of detection is higher (Heatwole 1968; Martín & López 1999; Cuadrado et al. 2001).

The wolf spiders used in this study are a light mottled brown color and blend in readily with the desert substrate where they are likely to be encountered. We believe, therefore, that the results of this study can be explained upon the basis of crypsis. In faster individuals, it may be advantageous to flee at farther distances, since there is a higher probability that the individual will survive entirely on the basis of escape speed. In slower individuals with less chance of escaping solely on the basis of speed, individuals may rely on crypsis to es-

cape detection. It may be advantageous for slower individuals to remain still, relying on crypsis for survival rather than fleeing and becoming more conspicuous to the predator.

Our results are similar to those obtained by Formanowicz et al. (1990) in ground skinks, *Scincella lateralis*. In individuals that had experienced tail loss 48 hours prior to testing, sprint speeds were significantly reduced, and individuals exhibited shorter flight distances. They interpreted the shorter flight distances in slower individuals to be the result of a behavioral compensation for tail loss. They suggested that autotomized individuals compensated for decreased speed by adopting a cryptic anti-predator strategy. This interpretation was based on information involving the relationship between flight distances and crypsis in lizards (Heatwole 1968; Bauwens & Theon 1981). Heatwole (1968) examined the relationship between flight distance and levels of crypsis in *Anolis* lizards. They found that cryptic species exhibited shorter flight distances than those that were less cryptic. Bauwens and Theon (1981) found similar results in gravid lizards, *Lacerta vivipara*. Gravid lizards compensated for decreased speed by adopting a cryptic anti-predator strategy.

In summary, maximum sprint speed was not significantly different for males and females, and maximum sprint speed was not significantly affected by the size of the individual. Furthermore, flight distance was not significantly related to size, but males tended to flee at a greater distance from a model predator. Sprint speed and flight distance were positively correlated. This positive correlation was considered to be the result of a trade-off between two alternative modes of predator avoidance: escape and crypsis.

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SEISMIC COMMUNICATION DURING COURTSHIP IN TWO BURROWING TARANTULA SPIDERS: AN EXPERIMENTAL STUDY ON *EUPALAESTRUS WEIJENBERGHI* AND *ACANTHOSCURRIA SUINA*

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ABSTRACT. During courtship, males of *Eupalaestrus weijenberghi* and *Acanthoscurria suina* performed body vibrations and palpal drumming after contacting conspecific female silk at the burrow entrance. Receptive females responded by leg tapping. To elucidate the communicatory channels involved in both species, courting males were placed in terraria with females that had burrowed. In the first experiment, the courting male was covered with a glass cup, minimizing airborne acoustic communication but allowing seismic communication. In the second, the male courted without the cup cover. In the third experiment, the male and the female were placed into two separated parts of the terrarium, greatly limiting seismic communication. In the fourth, these last parts were joined. Females of both species responded to the courtship with receptive behavior in all of the experiments except experiment 3. We conclude that male signals produced during courtship in these two species are mainly seismic. Male body vibrations (that would generate seismic signals) as well as female display, are a widespread phenomena in theraphosid spiders.

Keywords: Theraphosidae, seismic signals, male vibration, female sexual display

Spiders use different channels to communicate during courtship: chemical, tactile, visual and acoustic/vibratory (Krafft 1980; Uetz & Stratton 1983). Each channel has advantages and disadvantages in relation to the lifestyle of the animal and its environmental constraints. As a consequence of the potential nuptial cannibalism of spiders and the poor vision in most taxa, pressures of selection may have favored acoustic or seismic species-specific signals during courtship. An advantage of these signals is that they are relatively independent of environmental conditions (light, temperature, humidity) for efficiency of signal propagation (Foelix 1982; Krafft 1982; Redondo 1994). Another advantage is the temporal characteristic of the signal, which can be modified quickly according to the motivational state of the animal. Disadvantages include the short temporal persistence of the signal, and the high cost of production. The advantages could explain why acoustic/vibratory signals are so widespread in Araneae.

Acoustic/vibratory signals in spiders can be produced in three ways, according to Uetz & Stratton (1982): a) stridulation (22 families), b) percussion (six families) and c) vibration of structures (two families). Spiders may use air, water or substrate (ground, leaves, silk threads, etc.) for propagating vibrations. Stridulation and percussion have been studied in some species, but sometimes they are difficult to isolate from one another because a single motion can produce both signals, as happens in male palpal drumming. Some lycosids have a stridulatory organ located at the tibio-tarsal joint of each palp. Rovner (1967, 1975) found that, in some wolf species, palpal movement not only produced acoustic signals but also vibrations, which were transmitted into the substrate by means of specialized spines at the tip of the tarsal palp, a mechanism termed "substratum-coupled stridulation." Using playback techniques, Rovner discovered that females are capable of perceiving acoustic signals, but their responses are more intense when the speaker is laying on the ground. He concluded that female spiders orient better to substratum vibrations than to airborne sounds.

The third method of sound production, vi-

bration of structures, has been described in two species: by Rovner (1980) in *Heteropoda venatoria* (Linnaeus 1767) (Heteropodidae) and by Barth (1982) and Barth et al. (1988) in *Cupiennius salei* (Keyserling 1877) (Ctenidae). It consists of movements of the legs or abdomen, in such a way that the entire body vibrates. These movements produce vibrations which are transmitted via substrate (seismic communication).

A growing number of studies on sexual behavior of mygalomorphs (Coyle 1985, 1986; Coyle & OShields 1990; Jackson & Pollard 1990; Costa & Pérez-Miles 1998), and in particular from the theraphosid family (Baerg 1958; Minch 1979; Prentice 1992, 1997; Costa & Pérez-Miles 1992, 2002; Pérez-Miles & Costa 1992; Shillington & Verrell 1997; Yáñez et al. 1999) has revealed previously hidden intricacies in the mechanisms of communication employed by this group. As an example, 30 years ago it was believed that tarantula males initiated their courtship only after touching the females (Platnick 1971). Today we know that these males start courtship after detecting tactochemical cues associated with the female silk (Minch 1979; Costa & Pérez-Miles 1992, 2002; Prentice 1997; Shillington & Verrell 1997; Yáñez et al. 1999).

Eupalaestrus weijenberghi (Thorell 1894) and *Acanthoscurria suina* Pocock 1903 are burrowing theraphosids that have a widespread distribution in Uruguay. They are frequently sympatric, syntopic and synchronous, presenting a similar reproductive strategy (Costa & Pérez-Miles 2002). Their sexual periods occur during March and April, at the end of summer and beginning of autumn in the southern hemisphere (Costa & Pérez-Miles 2002). Mignone et al. (2001) and Costa & Pérez-Miles (2002) observed males of both species courting outside female burrow entrances after contacting conspecific female silk. Mignone et al. (2001) reported that females of *E. weijenberghi* responded to male courtship by displaying foreleg waving at the burrow entrance. Male courtship, either for *E. weijenberghi* or *A. suina*, was mainly characterized by Mignone et al. (2001) and Costa & Pérez-Miles (2002) as bouts of body vibrations while the male grasps the substrate with its legs. These vibrations apparently originate in the third pair of legs (unpublished data from restraining each pair of legs). According to these authors, courting males also perform palpal drumming, that can produce acoustic signals (airborne) as well as seismic signals (substrate borne). Theraphosid spiders possess stridulatory organs (Legendre 1963). Moreover, *A. suina* has stridulatory setae located retrolaterally at the trochanter of the palps (Pérez-Miles et al. 1996). Acoustic and or vibratory signals were suggested by Costa & Pérez-Miles (1992, 2002) as species-specific isolating mechanisms in theraphosids, as previously tested among Mesothelae species by Haupt & Traue (1986).

Our main objective was to find whether acoustic, seismic or both channels are involved in the courtship of *A. suina* and *E. weijenberghi*. Moreover, we described and analyzed elements of courtship by males and females for the two species.

METHODS

Materials.—Males were collected in the provinces of Canelones (Solymar Norte, 34° 45′ S, 56° 00′ W and Salinas Norte, 34° 45′ S, 55° 50′ W) and Montevideo (Melilla, 34° 45′ S, 56° 20′ W),Uruguay, during March 2002. For all experiments we used females of known reproductive history, which were collected from the same localities, between 1996 and 1999. As is well-known for Theraphosidae, adult females continue molting throughout their lives, so in each molt they become "virgin" (without sperm) again. All the females molted in the laboratory between December 2001 and January 2002. We used a total of 20 females and 20 males from each species. They were housed in glass jars of 9.5 cm diameter and 15 cm height, with soil as substrate and water provision. They were fed cockroaches (*Blaptica dubia*, Blattaria, Blaberidae) ad libitum. Voucher spiders specimens of both species were deposited in the entomological collection at the School of Sciences, Universidad de la República, Montevideo, Uruguay.

Experiments were carried out in glass terraria of 30cm x 16cm base x 20cm height, containing 6 cm of soil as substrate or, in the case of the third experiment, the aquaria were 15cm X 16 cm X 20cm. Females inhabited burrows in these terraria, which were constructed by us against the glass wall, allowing our observations. Each female walked along

the soil at night, so the silk with pheromone was widely released on the soil surface. We carried out experiments during March–May 2002, in coincidence with the reproductive period of these species in natural populations. All terraria were placed over polyurethane blocks in order to isolate animals from ground vibrations. Distances between males and females varied between 10–25 cm. For experiment three, ten glass terraria were built as two separated parts; one part contained the female burrow and the other only substrate. These "separated blocks" were later put together using an iron clamp, then being similar to an unitary block, contacting both soil and glass walls. In other experiments we used a thick glass cup, of 10 cm diameter and 10.5 cm height, which covered the courting male. For video recording, a Super VHS video camera was used. Sexual encounters were analyzed with a frame-by-frame video recorder in the Ethology Laboratory of the School of Sciences (Universidad de la República), Montevideo, Uruguay. The experiments were carried out at an average environmental temperature of 25.13 °C ± 1.05 SD.

Experimental design.—To test for the occurrence of acoustic (airborne) communication, a series of two consecutive experiments (A & B: see below) were carried out using the same ten pairs of female/male individuals of both species. For testing the occurrence of seismic (substrate borne) communication, another series of two consecutive experiments (C & D: see below) were carried out using a different set of ten pairs of female/male spiders of both species. Each pair of spiders was reused 1–7 days after the first experiment. Individuals were randomly assigned to pairs and experimental series. This design allows us to avoid the influence of individuality and/or subtle differences in the terraria (cut blocks, humidity). The observational time began when the male was placed in the terraria until female sexual display, or until 30 min, if there were no female response.

In the experiment A, or "cup block", a male was placed into a confined sector which occupied one third of the total surface of the terrarium, whereas a female inhabited her burrow in the other sector. A metallic grid with vertical bars separated 6mm from one another, impeded the access of the male to the female burrow. The male was covered with the glass cup, minimizing any possible acoustic communication. The experiment B, or "unitary block", was similar to A but no glass cup was used. In the experiment C, or "separated blocks", each terrarium was built as two separate parts: one containing the female in her burrow, the other, the confined male. The two parts, separated from each other by three millimeters, were set on polyurethane blocks, with each part located on separated tables, eliminating any possible seismic communication between male and female. During the night prior to the test, another female was located in the smaller container for depositing silk and pheromone. This female was removed before the trial. In this way when the male contacted the silk and pheromone during the trial, he responded with courtship. The experiment D, or "joined blocks", was similar to C, but in this case the two parts were pushed together, eliminating the gap, and joined with an iron clamp (Fig. 1).

Description and analysis.—The observed behavior of both females and males during the experiments was described and analyzed. The courtship behavioral units of males and females were described from the experiment B for both species, because this group best reflected what occurs in nature. Normality and homogeneity of variance of continuous variables (durations of the behaviors) were tested using the Kolgomorov- Smirnov and Cochran C-test, respectively. Non parametric Mann-Whitney U-test, the one sample and two samples Chi-square tests were used for frequencies and non- parametric durations. The McNemar test for the significance of changes was used for dependent samples (A vs. B and C vs. D), but when the expected frequency was less than 5, the Binomial test was used. All statistical analyses were performed using free software programs (http:/www.r-project.org).

RESULTS

Courtship.—Male courtship of both species was characterized by the alternation of periods of activity and inactivity. Activity consisted mainly of body vibrations and palpal drumming. Male body vibrations were caused by spasmodic contractions of legs, apparently by the third pair. During vibrations, tarsal claws were fixed to the ground. Vibration was complex, its intensity was very var-

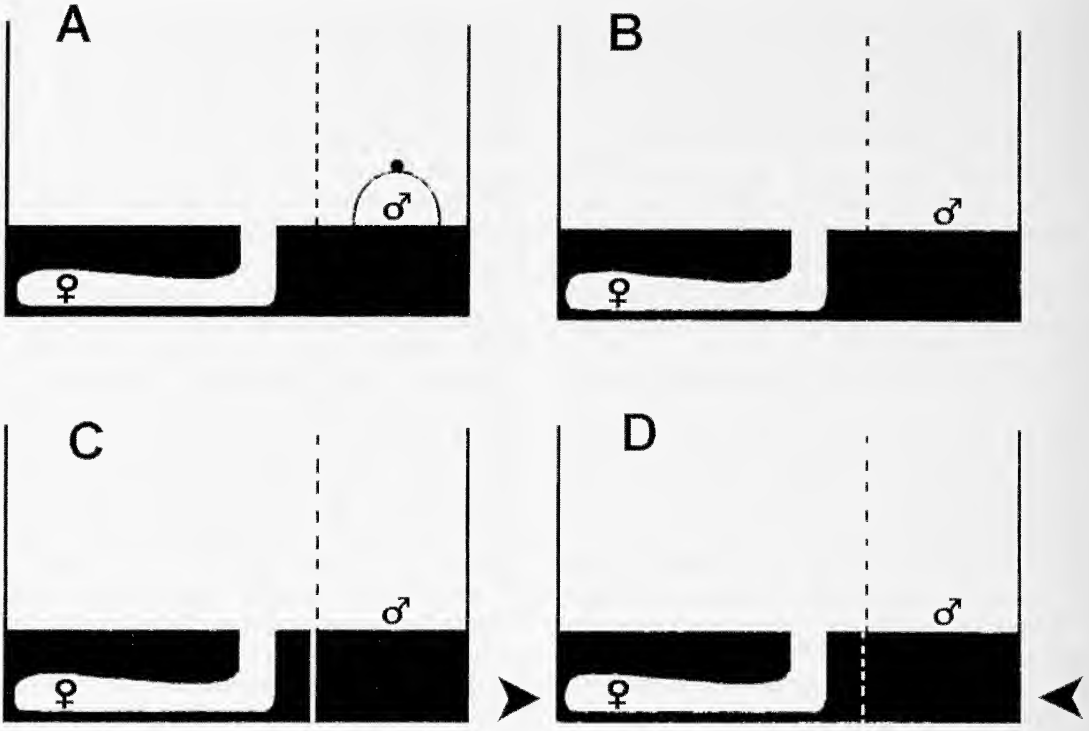

Figure 1.—Schematic drawings showing the experimental design used for the two Theraphosidae species. Broken vertical lines represent the metallic grid separating the male from the female. Each male was placed on the soil, while each female remained inside her burrow. Experiment A = cup block, experiment B = unitary block, experiment C = separated blocks, experiment D = joined blocks.

iable, and could not be quantitatively described using the video register because it was not possible to observe male movements in detail. However, vibrations seem to be of low frequency. Palpal drumming consisted of alternative, soft 'cycling movements' of the palps on the substrate. Both body vibrations and palpal drumming, in general, were alternated but sometimes they took place synchronously, mainly when the body vibrations were of low intensity. Bouts of vibration and drumming were considered together when analyzing the durations of active courtship periods of males. Tables 1 & 2 show the mean durations of these bouts until female response for the two species. Mean duration of bouts of vibration and drumming was approximately seven seconds for both species.

Females of both species showed their characteristic sexual display inside the burrows, tapping vigorously with the first and second pair of legs against the substrate, immediately after a male bout. In frame-to-frame video analyses, females of both species showed the following displays: leg flexing, lifting and lowering, contacting the ground. In some cases, the percussion was audible to the observer. Two latencies were considered: Latency 1 was from the end of the last male signal bout until female leg tapping, and Latency 2 from the end of the first male bout until female leg tapping. Some females responded immediately after the first bout; thus, these two latencies are equal (Tables 1 & 2). Mean number of leg movements during the first bout of female leg tapping, as well as the number of female bouts of leg tapping during the whole experimental period, are shown in Tables 1 & 2. After female responses, males frequently changed their behavior. In *E. weijenberghi*, 6 of 10 males oriented to the female burrow, 2 of 10 increased their locomotive rate without orientation and 2 of 10 showed no response to the female call. In *A. suina*, 8 of 10 females responded to male courtship. Two of 8 males oriented to the female burrow, 2 of 8 increased their locomotive rate and 4 of 8 showed no responses.

Table 1.—Courtship characteristics of *Eupalaestrus weijenberghi* (experiment B). Male courtship duration includes both vibrations and palpal drumming until female response. Latency 1 = latency from the end of the last male signal to the first leg tapping of the female. Latency 2 = latency from the end of the first male signal to the first leg tapping of the female. Leg movements = number of movements of one leg during female leg tapping. Leg tapping = number of female bouts performed during the whole experiment.

Pair	Courtship (sec)	Latency 1 (sec)	Latency 2 (sec)	Leg movements	Leg tapping
1	9	1	1	15	4
2	15	1	4	21	2
3	11	0	6	13	4
4	2	1	1	14	2
5	5	3	53	5	7
6	9.5	1	83	14	4
7	4	1	1	22	3
8	5.75	3	53	11	2
9	4	1	22	15	1
10	2	1	53	16	3
Mean ± SD	6.7 ± 4.3	1.3 ± 0.9	27.7 ± 30.2	14.6 ± 4.8	3.2 ± 1.7

When comparing mean durations of male signaling bouts (vibration + drumming) between species, both before first female response, no significant differences were found using the Mann-Whitney test ($U = 30.5$, $P = 0.397$). No statistical differences were found either when comparing the latency of female response to the last bout of a male ($U = 20.5$, $P = 0.083$), or when comparing latency to the first male bout ($U = 34$, $P = 0.60$). The number of movements during female leg tapping was greater in *E. weijenberghi* than in *A. suina* ($U = 17.5$, $P = 0.04$); the number of bouts of female leg tapping was also higher in *E. weijenberghi* ($U = 15$, $P = 0.03$).

Communicatory channels.—The number of female responses from the four experiments are given in Table 3. All the females of *E. weijenberghi* belonging to experiments A, B and D responded to male courtship. On the other hand, in *A. suina* 7 of 10 responded to male courtship in experiment A, 8 of 10 in B, and 4 of 10 in D. In separated blocks (experiment C), none of the *E. weijenberghi* nor *A. suina* females showed responses to male courtship. Observed versus expected Chi-

Table 2.—Courtship characteristics of *Acanthoscurria suina* (experiment B) corresponding to the eight cases where females responded. Male courtship duration includes both vibrations and palpal drumming until female response. Latency 1 = latency from the end of the last male signal to the first leg tapping of the female. Latency 2 = latency from the end of the first male signal to the first leg tapping of the female. Leg movements = number of movements of one leg during female leg tapping. Leg tapping = number of female bouts performed during the whole experiment.

Couple	Courtship (sec)	Latency 1 (sec)	Latency 2 (sec)	Leg Movements	Leg tapping
1	7	0	0	6	1
2	11.3	0	0	8	1
3	7	0	21	6	2
4	7.3	3	26	14	4
5	6.1	1	436	19	2
6	5	0	38	10	1
7	7.3	1	67	5	1
8	8	0	110	6	1
Mean ± SD	7.4 ± 1.8	0.6 ± 1.1	87.3 ± 145.6	9.3 ± 4.9	1.6 ± 1.1

Table 3.—Number of females that performed leg tapping in response to the male courtship in the four experimental groups.

	E. weijenberghi		*A. suina*	
	Leg tapping	No leg tapping	Leg tapping	No leg tapping
Cup block (A)	10	0	7	3
Unitary block (B)	10	0	8	2
Separated blocks (C)	0	10	0	10
Joined blocks (D)	10	0	4	6

square test among the four experiments (assuming 50% as expected value) showed significant differences for *E. weijenberghi* (χ^2 = 10, $P < 0.019$, df = 3) and also for *A. suina* ($\chi^2 = 8.16$, $P < 0.043$, df = 3). The female response in experiment C is significantly different from response in B for both species (for *E. weijenberghi*, $\chi^2 = 16.20$, $P = 0.0001$, df = 1; for *A. suina* $\chi^2 = 10.21$, $P = 0.0014$, df = 1). In *E. weijenberghi*, experiments A and B were identical ($P = 1$, Binomial test), but significant differences were found between C and D ($\chi^2 = 10$; $P < 0.001$) with the McNemar test. Experiments B and D were identical ($\chi^2 = 0$, $P = 1$, df = 1) using the Chi-square test in this species. In *A. suina*, there were no significant differences between A and B ($P > 0.31$) with the Binomial test, nor between C and D ($P = 0.16$). There were no differences between B and D ($\chi^2 = 1.880$, $P = 0.17$, df = 1) using the Chi-square test.

DISCUSSION

Our main objective was to determine experimentally what communicatory channel is mainly used during courtship for the focal species. Rado et al. (1989) demonstrated, using a similar experimental design, that the Mole Rat, *Spalax ehrenberghi*, communicates by seismic signals. In *E. weijenberghi* the results clearly showed that separated blocks (experiment C) prevented the transfer of seismic signals between the sexes, whereas communication was unimpeded in the other treatments.

The females which showed no response in separated blocks, all responded to male courtship once these blocks were joined (experiment D). Thus, we conclude that communication through the substrate (seismic communication) is present during courtship. Moreover, the absence of female response in separated blocks also indicate that airborne acoustic communication, is not important; at least at the experimental distances used in this study. Absence of acoustic communication is also supported by the lack of differences between unitary and cup blocks. Hence, seismic signals are sufficient to elicit a complete female response during the courtship of *E. weijenberghi*.

The results of *A. suina* were similar to those of *E. weijenberghi*, indicating that they also use the seismic channel for communicating during courtship. The main difference in the *A. suina* was in the non–significant differences between separated and joined blocks (experiments C & D). This could be explained by a lower intensity of the male vibration in *A. suina* (Quirici, unpub. data) and/or less responsiveness from conspecific females than those of *E. weijenberghi*. Acoustic communication in *A. suina* seems not to have an important role in sexual communication, as in *E. weijenberghi*, results from unitary and cup blocks were similar. Due to the presence of a putative stridulatory organ on the palpal trochanter of *A. suina*, the occurrence of acoustic communication would appear reasonable. However, occasional observations in the field showed that males spend a long time performing palpal drumming at the burrow entrance. Acoustic communication could be possible when males reach the burrow entrance, thus avoiding possible obstacles that could deform or interrupt a delicate acoustic signal. Therefore, an acoustic channel of communication could be functional at short distances.

Male vibrations in courtship appear to be a widespread behavior observed in many Theraphosidae spiders, first reported by Gerhardt (1929). Minch (1979) described this behavior as body oscillations; Shillington & Verrell (1997) called it "quiver"; Yáñez et al. (1999) called it "shaking"; Costa & Pérez-Miles

(1992, 2002) and Pérez-Miles & Costa (1992) named it "body vibrations". Prentice (1992, 1997) termed the behavior "stridulating vibration" and found that the signals could be perceived by the female up to 1.2 m distance on a heterogeneous substrate. Moreover, he reported that stridulation was audible by the observer under laboratory conditions in *Aphonopelma joshua* Prentice 1997. However, these vibrations remind us of the third method of sound production postulated by Rovner (1980), "vibration of structures", but not the stridulatory method. Some tests (unpub. data) in which we tied the third pair of legs and in others tied the second pair of legs (control), showed that the third pair would be responsible of the vibrations (a geophone did not register vibrations when the third pair was tied). According to our findings, the Theraphosidae would communicate by "vibration of structures". All authors postulate a communicative role for this behavior, alerting the female of male presence. The possible function of the vibration as a way of transmitting a species-specific signal through the ground was postulated by Haupt & Traue (1986) for Mesothele, and by Costa & Pérez-Miles (1992, 2002) for Mygalomorphae. Preliminary observations, however, have shown some degree of confusion in sexual communication between *E. weijenberghi* and *A. suina* in the laboratory. This opens an exciting field of research because, as was previously mentioned, these species are sympatric and synchronous and share similar reproductive strategies.

Leg tapping of burrow-occupying females was observed only as a response to male courtship, indicating a receptive state. It was first observed by Prentice (1992) in three species of *Aphonopelma*, who called it "drumming". We found that both *E. weijenberghi* and *A. suina* respond to male courtship from inside their burrows. Female leg tapping would not only inform the male about her willingness to copulate, but also help the male to orient towards the burrow entrance. *Eupalaestrus weijenberghi* males seem to orient more easily than *A. suina* males for the calling female, probably due to the vigorous *E. weijenberghi* female responses. This behavior is possibly more widespread than previously supposed, since female behavior is often unobservable inside the burrow. For example, Prentice (1997) reported females of another *Aphonopelma* species performing leg tapping, and Yáñez et al. (1999) observed females of *Brachypelma klaasi* (Schmidt & Krause 1994) shaking.

Burrowing tarantulas share similarities with other subterranean species in some of their ways of communication, independent from phylogenetic constraints. Compared to acoustic signals, seismic signals have the advantage of propagating through long distances and at speed two–five times faster than the acoustic signals, depending on the type of soil and degree of soil moisture (Rado et al. 1989). Taking into account the advantages of seismic signals, the widespread occurrence of male body vibration, the probable female seismic response, and the absence of costly specialized emission organs, we suggest that seismic signals are the main communicatory channel used by burrowing Theraphosidae during courtship.

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MATING AND SELF-BURYING BEHAVIOR OF *HOMALONYCHUS THEOLOGUS* CHAMBERLIN (ARANEAE, HOMALONYCHIDAE) IN BAJA CALIFORNIA SUR

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ABSTRACT. The spider *Homalonychus theologus* is endemic to desert zones from southwestern California to southern Baja California Peninsula. Until now little has been published about its biology. In this paper we describe the reproductive and self-burying behavior and some aspects of the ecology of the species. Courtship behavior is between levels I and II, and the copulation position is a modification of type III. The male wraps the female's legs in silk before mating. This behavior could help justify inclusion of the Homalonychidae in the superfamily Lycosoidea. Possible camouflage behavior was attributed to the observation that these spiders can camouflage themselves by adhered sand grains to their bodies and buried themselves in the substratum. Females constructed eggsacs two days on average after mating one eggsac contained 29 eggs and other zero. Females incorporated sand "collars" to the egg sac with silk, probably as protection for the eggs against the dry environment as well as camouflage. This activity was carried out within 34 hours before oviposition. In the field, solitary spiders were found mainly under dead fallen cacti *Pachycereus pringlei*.

RESUMEN. La araña *Homalonychus theologus* es endémica de las zonas desérticas del sur de California hasta el sur de la península de Baja California. Hasta ahora se conoce poco acerca de su biología. En este artículo describimos los hábitos reproductores, conducta de enterramiento y aportamos algunos datos ecológicos de esta especie. La conducta de cortejo es intermedia entre los niveles I y II y la posición de cópula corresponde a una modificación del tipo III. El macho envuelve las patas de la hembra con seda antes de la cópula. Esta conducta puede contribuir a que las Homalonychidae puedan ser incluidas en la Superfamilia Lycosoidea. La posible conducta de enterramiento fue registrada cuando las arañas incorporaron granos de arena a sus cuerpos y se enterraron en el sustrato. Las hembras fabrican sus ovisacos pocos días después del apareamiento con un promedio de dos días en su elaboración y el número de huevos observado fue de 0–29 por ovisaco. Las hembras incorporan "collares" de arena con seda al ovisaco como una probable protección de los huevos a la desecación del medio. Este evento fue llevado a cabo en 34 horas. En el campo, las arañas se encontraron principalmente solas y bajo cardones en descomposición *Pachycereus pringlei*.

Keywords: *Homalonychus*, Baja California, mating behavior, self-burying behavior

Homalonychus theologus Chamberlin 1924 is one of two homalonychid species endemic to North America. This family is distributed in the warm deserts of southwestern United States and northwestern Mexico (Gertsch 1979; Roth 1984). *Homalonychus theologus* is found from southern California to southern Baja California Peninsula, on the adjacent islands Cedros and Margarita in the Pacific Ocean, and on several islands in the Gulf of California (Roth 1984); it is considered endemic to these regions.

Homalonychids are wandering spiders usually found in fine sand or soil, under loose boulders, boards or detritus. Only females and immatures cover their bodies with fine soil, which adheres to the setae of their integument (Roth 1984). *Homalonychus theologus* may mimic dry cactus spines by joining their legs in pairs as a potential defensive response.

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They cover the egg sacs with fine sand, probably to avoid predation (Vetter & Cokendolpher 2000).

Although *H. theologus* appears to be one of the most numerous spiders in the Baja California Peninsula and adjacent islands (Roth 1984), only one short paper (Vetter & Cokendolpher 2000) focused on the biology of this species, and another on the taxonomy of the family Homalonychidae (Roth 1984) has been published. In this paper, we examine mating and self-burying behavior of *H. theologus*.

METHODS

Spiders were collected at two sites in the Cape region of southern Baja California Peninsula: El Comitán and San Pedro, located at 24°08′7″N, 110°25′52″W and 23°54′44″N, 110°15′8″W, respectively. The local climate is very dry to semidry with rain in summer only and median annual temperatures from 22–28 °C (García 1973). Vegetation is sarcocaulescent scrub consisting mostly of "cardón" *Pachycereus pringlei* and "cholla" *Opuntia cholla* (León de la Luz et al. 1996).

Collections were taken weekly in El Comitán from 1200–1400 h, from August 2000–June 2001. Spiders were collected by hand from under decaying cardons and other cacti. Each spider was transported individually in a 250 ml plastic jar to the laboratory. Voucher specimens of *H. theologus* were deposited in the arachnid collection of the CIBNOR.

In San Pedro, spiders were collected in August, October and November 2000, and January 2001 for behavior observations under laboratory conditions. The microhabitat of spiders at both sites was described, and the number of specimens captured at each site was recorded. A total of 57 immature and adults were maintained in the laboratory and were used for behavior studies. Spiders were kept always in a dark 1.87 × 2.00 m room with temperature 23–27 °C and relative humidity 50–60%. Observations of mating behavior were made from 6 March–17 April 2000 between 1000–1300. Sixteen male/female pairs were used. Females were introduced to a 22.7 × 20.5 cm glass container at 26.2 °C and 46.8% relative humidity with fine soil as a substrate; males were introduced 1 hr later; each pair was permitted to mate, after which females were placed individually in transparent 250 ml plastic jars. Fine soil was placed in the bottom of each jar as substrate, with a piece of dry cactus as retreat and a small container of wet cotton for water. Each jar was covered with fine weave cloth. Mating time was recorded. If a pair didn't mate within 10 minutes, one of the pair was replaced by another of the same sex.

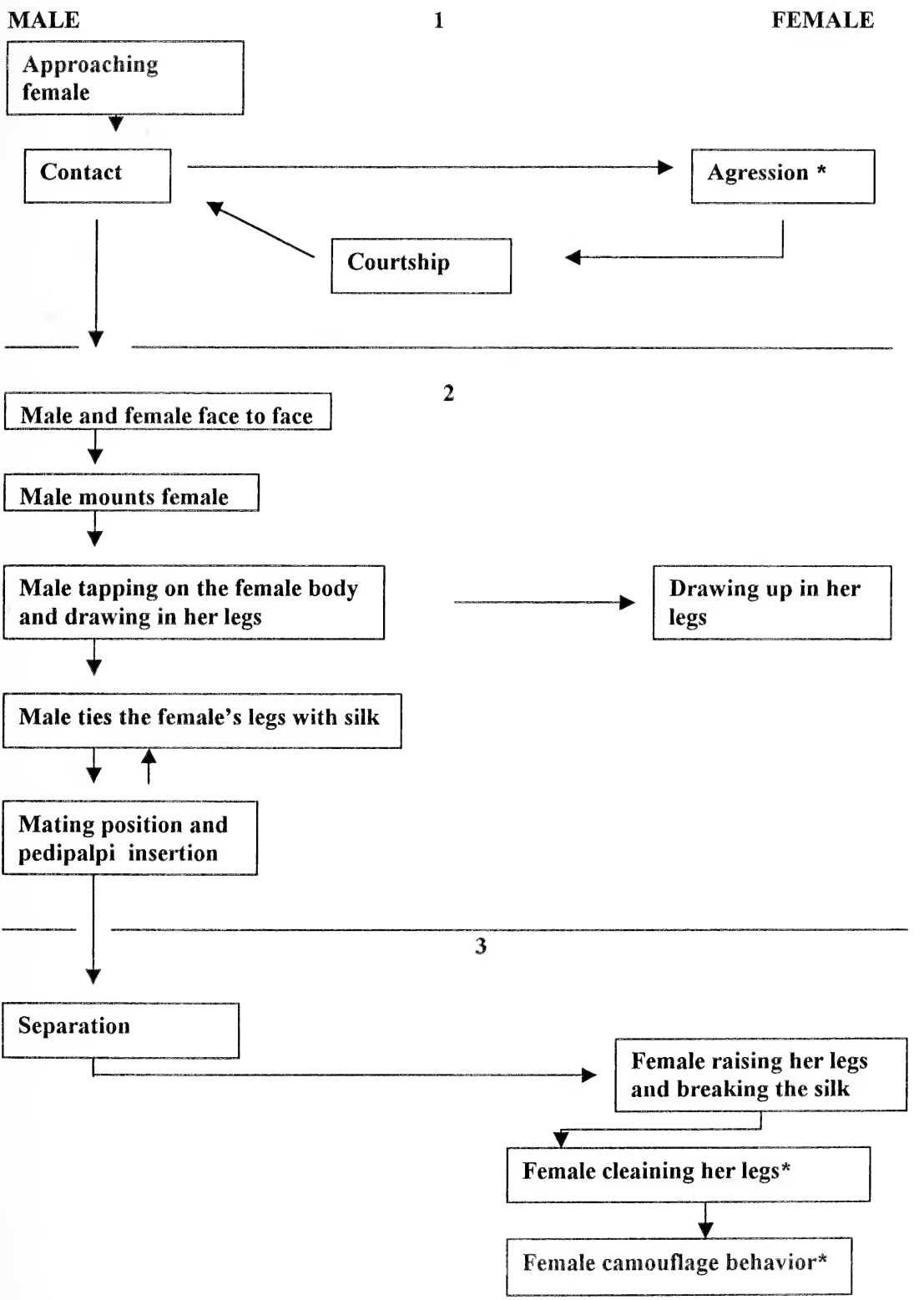
Adults and immatures were fed weekly with *Tenebrio molitor* L. larvae. The time during pre-oviposition, oviposition, number of egg sacs per female was recorded. Self-burying behavior was recorded for 27 recently molted spiders. These observations were recorded once with an RCA CCD video camera, with a 24x200m 100x eyepiece in natural light, and photographs were taken with a MINOLTA Dynax 8000i camera.

RESULTS

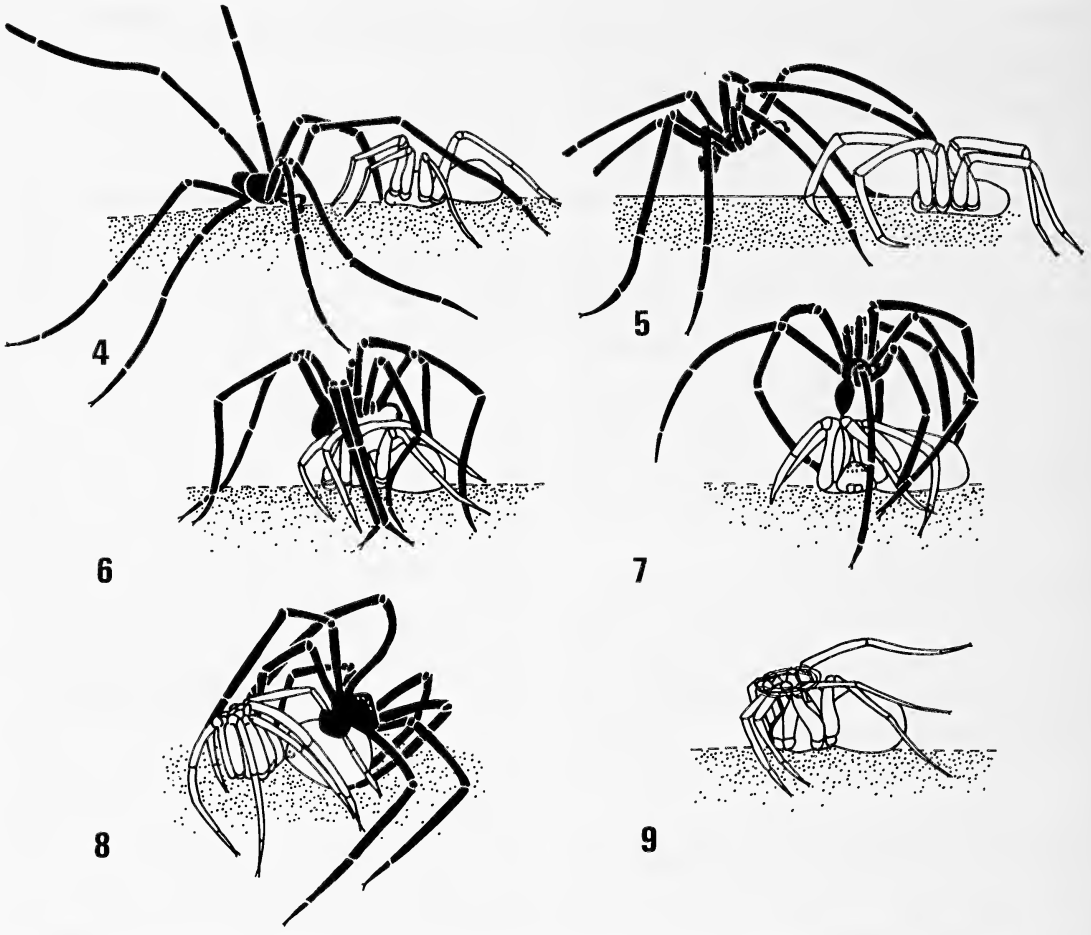
Field observations.—In both localities, 94% (n = 385) of the spiders were found under sections of fallen *Pachycereus pringlei* cacti, from 5 × 3 cm to 250 × 30 cm of size. Two percent (n = 9) of spiders were found under dead tree trunks, 2% (n = 7) under cartons, and 2% (n = 8) in crevices between cacti. Eighty-four percent of the spiders were found alone, 12% were grouped in pairs; and 3% were in threes. Of all spiders, 97% were found on the sand under cacti, 2% burrowing in soil and only 1% were observed in the paired leg formation. All captured spiders were found camouflaged with sand grains. At El Comitán sub-adults and females of *H. theologus* were present in October and November, whereas immatures were active all year and maintained an almost constant population size.

Mating behavior.—Courtship and mating behaviors of eight pairs of adult spiders were observed (8 males, 5 females were matured in the laboratory and then mated, 3 females of unknown mating status were captured in the field.). Sperm induction by males was not observed, but small triangular webs were attached to the jar walls indicated probable filling of palps with sperm. Sexual behavior was divided in to three stages: pre-copulation, copulation and post-copulation (Figs. 1–3).

Pre-copulation: The male approaches the female (Fig. 4), drums his palpi in an alternating sequence and attemps to mount her. If the female is not receptive, she attackes him (Fig. 1). Then the male courts by moving his



Figures 1–3.—Mating behavior of *Homalonychus theologus*. 1. Pre-copulation behavior. 2. Copulation behavior. 3. Post- copulation behavior. Asterisk means behavior observed only in some individuals (see text).



Figures 4–9.—Mating behavior of *Homalonychus theologus*. 4. M ale approaching to female. 5. Male tapping palpi and front legs on female's body. 6. Male drawing female's legs above her carapace. 7. Frontal view of male circling female's legs with silk. 8. Male and female mating. 9. Lateral view of female with the silk circle after mating.

front pairs of legs alternately up and down tapping the substratum, walking a few steps and stopping. The male repeats the sequence several times until he stands again in front of the female. This behavior was observed in only two males. Mean approach time was 11.3 min ± 23.6 (range 0–68.4 min, n = 8).

Copulation: When the female was receptive, she remained motionless on the substratum (Fig. 5) while the male mounted her, tapping his palpi on her carapace and tapping his front pairs of legs on her abdomen. During this process, the female adopted a passive posture, drawing her legs in close to her body so that the patellae of her legs almost touched one another above her carapace while the male helped her to maintain this position with his third pair of legs, resting only his fourth pair of legs on the substratum (Fig. 6). He immediately began spinning silk threads in a ring around the patellae and tibiae of the female to keep them together (Fig. 7). When she was well tied, the male leaned to the right or left side of the female for the mating position (Figs. 3, 8). The left palp was inserted in the left side ($\bar{x}$ 1.5, SD ± 1.2), and the right palp in the right side ($\bar{x}$ 2.6, SD ± 2.3) alternately several times. With each insertion, the male produced fast vibrations with the second and third pairs of legs. He added more silk threads to the ring, mated again and repeated the behavior. Mating lasted approximately 3.6 min (range 0.5–13.3 min, n = 8).

Post-copulation: After mating, the male ran

away rapidly and the female remained motionless for few seconds on the substrate (Fig. 9) suddenly breaking the silk circle, raising and extending her legs. Six of the 8 females cleaned the silk from their legs and rubbed them together. After mating, two females displayed the self-burying behavior, which is described later. Only two males tried mating again with mated females and only one of these was successful.

Of eight mated females, only two made egg sacs. The process was observed once. One egg sac was constructed under a fragment of cactus on the day following mating. The other was attached to the wall of a jar eleven days after mating.

Egg sac construction.—One female spun a silk sheet on the lateral wall of the container. After that, she attached silk threads with sand grains like "collars", made by moving her spinnerets from side to side on the substratum secreting silk to affixed small sand grains added to the spinnerets and then onto the silk sheet. She repeated this behavior to make the upper wall of the egg sac taking the form of a dome. Then she held herself with her two front pairs of legs to the inner wall of the dome, standing in a vertical position. In this position she continued making silk collars with sand grains, then she stopped this behavior and with the sand collars attached to her spinnerets, and still in vertical position she pushed herself to the top of dome adhering the sand collars in the outer wall, secreting silk threads to strengthen it. From time to time the female scratched in the sand on the bottom of the container, throwing sand grains with her two front pairs of legs and continued making collars, repeating the behavior described previously. Although it could not be seen how the egg sac was finished, this behavior was repeated until an opening in the lower rim was left, where she entered and covered the inside with silk. After 34 hrs the egg sac was finished, and the female deposited eggs for 30 minutes. She remained inside 13.5 hours more; then came out and closed the opening of the egg sac. The emergence of the immatures three months later was not observed. When the egg sacs were opened, one of them was empty and the other had 29 desiccated eggs.

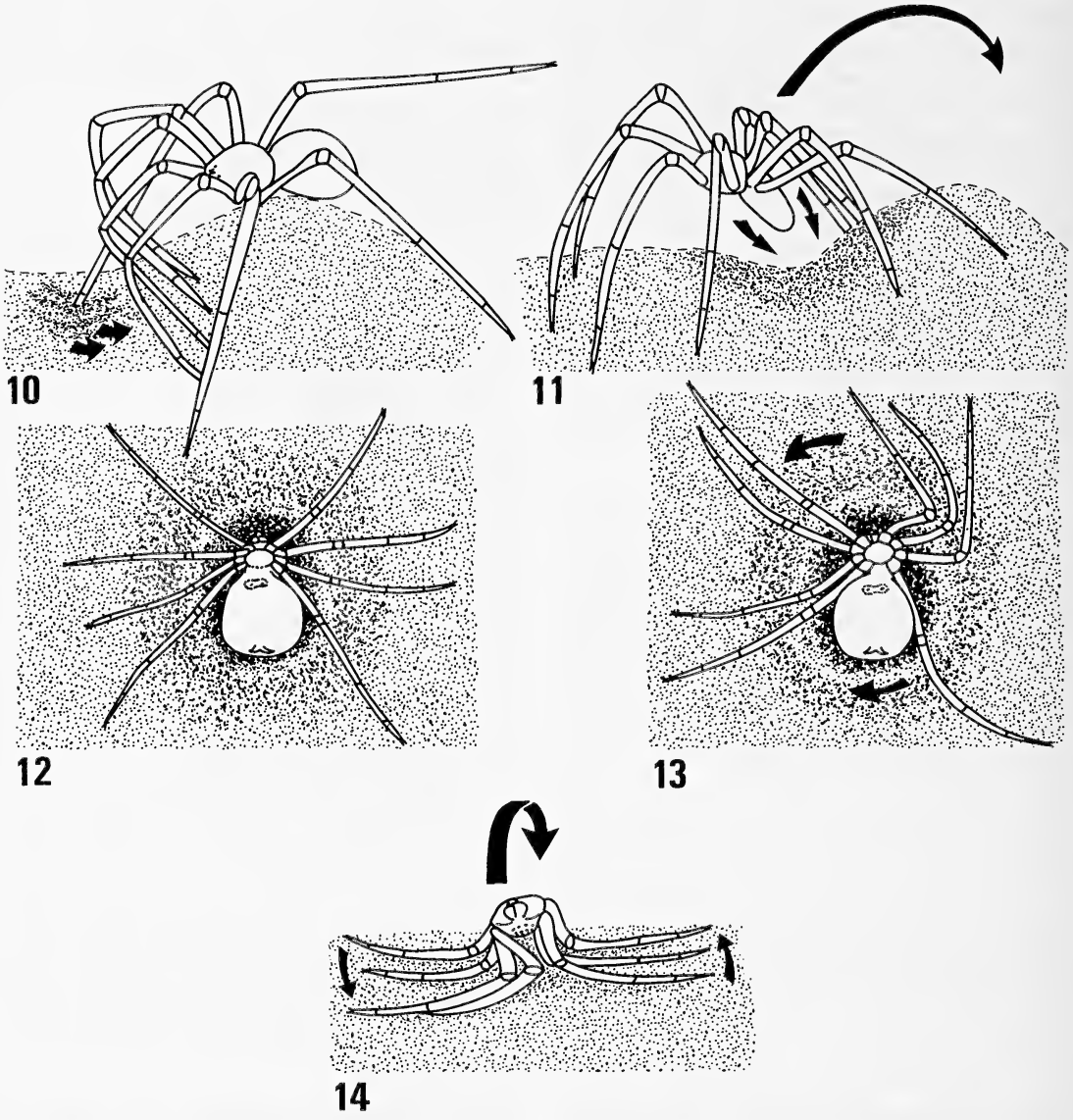
Self-burying and possible defensive behavior.—Under laboratory conditions observations were recorded on 27 recently molted spiders. To cover their bodies with sand, spiders scratched in the sand substrate with their palpi and first two pairs of legs, throwing sand grains from underneath the abdomen and making a small cavity (Fig. 10). They jumped and put their abdomen inside the cavity (Fig. 11). With their bodies in a vertical position, the spiders lay down on the sand mound with their ventral side up (Fig. 12). In this position, the spiders rocked their bodies slowly and continuously from side to side (Fig. 13). Then they flexed all their legs back and shook them from the patellae to the tarsi (Fig. 14). Finally they jumped up and in dorsal position placed their bodies on one side and extended the legs of the opposite side, shaking them rapidly back and forth in the sand. They scratched the sand substrate and repeated the behavior. Finally they expanded all their legs on the other side of their bodies and stood up totally covered with sand. Each spider performed this behavior twice (n = 26) with one spider performing it 7 times. This behavior was observed from the fourth instar to adult with the exception of adult males.

In captivity, almost all spiders of every instar burrowed in the soil. This behavior is different from described above and was recorded once as follows: The spider scratched in the sand with her two front pairs of legs, making a cavity. Then she jumped down and covered herself, throwing sand with her fourth pair of legs until completely buried. Then she extended her legs, moving them back and forth until they were outstretched and completely covered with sand.

Quiescent spiders and those collected in the field placed their legs in a rigid paired formation: the first two pairs forward and the last two pair backward, giving the appearance of dead cactus spines, according to Vetter & Cokendolpher (2000). When a spider was held by the leg with a pair of forceps, it rapidly autotomized the leg.

DISCUSSION

Field observations.—In San Pedro and El Comitan, spiders were found mainly under dead fallen cacti because rocks and stones are scarce in these habitats. In similar habitats *H. theologus* has been found under big rocks, loose boulders, boards and detritus (Roth 1984); but Vetter & Cokendolpher (2000) re-



Figures 10–14.—Self-burying behavior of *Homalonychus theologus*. 10. Lateral view of *H. theologus* scratching in the sand, forming a mound. 11. Lateral view of *H. theologus* putting its abdomen in the cavity. 12. Upper view of *H. theologus* with her ventral body up on the sand mound. 13. Upper view of *H. theologus* rocking its body from side to side on the sand mound. 14. Frontal view of *H. theologus* flexing her legs back and shaking them up and down in the sand. Arrows indicate the movements of *H. theologus* legs and body on the sand surface.

ported that the spiders were very scarce during daytime and speculated that they spend the daytime in rodent burrows and under rocks.

Mating behavior.—Sperm web structure of *H. theologus* males was similar to that described by Foelix (1996). When males were ready to reproduce, they rested on the substratum the container, presumablely searching for females; if they were not ready to mate, they remained suspended at the top of the container.

Homalonychus theologus courts at level I according to the classification of Platnick (1971) because it requires direct contact between male and female, but the courtship level could be between I and II because like lycosids, pisaurids and sicariids, the male of *H. theologus* probably detects the female by

some type of chemical stimulus, but this could not be verified in this study. The mating position of this species is a modification of type III position used by most hunting spiders, such as pisaurids, lycosids and thomisids (Foelix 1996). The male behavior of tying the female with strands of silk before or during mating has been recorded in other spiders such as the thomisid *Xysticus*, the philodromid *Tibellus* (Platnick 1971), the theridiid *Latrodectus* (Stern & Kullmann 1981), the dictynid *Dictyna* (Starr 1988) and the oxyopid *Oxyopes* (Preston-Mafham 1999). Similar bonds also are used by tetragnathid *Nephila maculata* (Fabricius 1793): the male places threads among the legs, the base of the abdomen and the carapace of the female (Robinson & Robinson 1980). The mating position assumed by *H. theologus* is very similar to that of the pisaurid *Ancylometes bogotensis* (Keyserling 1877) (Merrett 1988) in that the female's legs are trussed up tightly over the carapace. The male of *A. bogotensis* spins two silk rings, an outer ring around the distal ends of the front tibiae and an inner ring around the patellae (Merrett 1988). In the pisaurid *Pisaurina mira* (Walckenaer 1837), the male spins threads only between legs I and II of the female (Bruce & Carico 1988). Probably the male ties the female with silk to supress predation by the female during mating as has been the most consistent suggestion, although Foelix (1996) states that this behavior has symbolic significance only. Nevertheless Preston-Mafham (1999) suggests that producing the wrapping by the male is an important behavior and it seems highly likely that the silk plays a principal role in preparing the female physiologically and behaviorally for copulation. Post copulation behavior of the *H. theologus* female was similar to that observed in *A. bogotensis*, in which the female releases herself and cleans the silk from her legs (Merrett 1988).

Considering that courtship and mating behavior is an important phylogenetic character, it is possible that *H. theologus* is closely related to Pisauridae species, because the males of both tie the female with silk threads prior to copulation. Previously Homalonychidae was included in Pisauroidea (Lehtinen 1967) because they share some morphological characteristics with Oxyopidae and Pisauridae, such as eye pattern, feathery hairs, notched trochanters, and basic appearances of male and female genitalia. Nevertheless Roth (1984) argued to retain the Homalonychidae as a separate family because those characteristics are insufficient as justification to include this family in the Pisauroidea. Later Coddington & Levi (1991) grouped Oxyopidae, Pisauridae and Lycosidae, which share synapomorphies of male palp structure with other families in the super family Lycosoidea. We think that although homalonychid spiders have been isolated and restricted to the arid zones of the southwest USA and northwest of Mexico, its reproductive biology, genitalia and other morphological characteristics indicate a relationship with this family and therefore could be included in the super family Lycosoidea proposed by Coddington & Levi (1991).

Egg sac construction.—There are parallels among aspects of the behavior of *H. theologus* and the sicariid *Sicarius peruensis* (Keyserling 1880) because both are predominantly desert spiders. The construction of the *H. theologus* egg sac is similar to that of *S. peruensis* in that both species incorporate silk threads with sand grains. The size, form and texture of egg sacs are notably different between the species, as well as in the time for its construction and oviposition. It is interesting to point out that *S. peruensis* throws sand to bury the egg sac (Levi & Levi 1969), while *H. theologus* only attaches the eggsac to the substratum (Vetter & Cockendolpher 2000). This was verified in the field when an egg sac was found under a fallen dry cactus, and was so similar to the substratum that it was difficult to identify.

We agree with Vetter & Cokendolpher (2000) that it could serve to protect the eggsac against predators and parasites, but also to prevent it from desecation in the dry environment. During this study, none of the other females made egg sacs, but Vetter & Cokendolpher (2000) recorded two egg sacs per female. If our results and those of other authors are considered, females of *H. theologus* produce from 20–30 eggs per sac.

Self-burying and possible defensive behavior.—This behavior has been observed in other spiders such as *Sicarius* sp. (Sicaridae), but spiders of this species throw sand on the body when burrowing in the substratum (Reiskind 1965). Other spiders of the genera *Cryptothele* (Zodariidae), *Paratropis* (Paratro-

pididae), *Microstigmata* (Microstigmatidae), and *Bradystichus* (Bradystichidae) and the opilionid *Trogulus* (Trogulidae) have similar habits (Roth 1984). This behavior probably is an adaptation of these arachnids, including *H. theologus*, to protect themselves from predators although could it also serves as thermoregulatory function. This type of primary defense is of great importance in arid zones and deserts because there is relatively little vegetation cover to protect against predators (Cloudsley-Thompson 1996). The behaviors of leg autotomy and pairing of legs observed in *H. theologus* both belong to a secondary type of defense, effective when the spiders are threatened by predators (Cloudsley-Thompson 1995). Nevertheless *H. theologus* is mainly nocturnal like most other desert-dwelling spiders, therefore, a visual defense may be effective only in full moonlight, so sand camouflage could has obvious advantages however the leg pairing behaviour is more difficult to imagine functionally.

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NOTES ON THE GENUS *BRACHISTOSTERNUS* (SCORPIONES, BOTHRIURIDAE) IN CHILE, WITH THE DESCRIPTION OF TWO NEW SPECIES

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ABSTRACT. Two new species of *Brachistosternus* from Chile are described. *Brachistosternus* (*Leptosternus*) *cekalovici* new species can be distinguished from most other species of the genus because the divided dorsal gland of the telson. The closest species are *B.* (*L.*) *artigasi* Cekalovic 1974 and *B.* (*L.*) *negrei* Cekalovic 1975, for which redescriptions are provided. *Brachistosternus cekalovici* has only been collected in "Tres Cruces", Coquimbo Province, Chile. *Brachistosternus* (*Leptosternus*) *mattonii* new species is also described. This species is most closely related to *B.* (*L.*) *donosoi* Cekalovic 1974, from which it can be distinguished by its more densely granular tegument (especially on the ventral surface of the metasoma), hemispermatophore with more developed internal spines, and the lack of a telson gland. A redescription of *B. donosoi* is also provided. Both species are related to the Argentine plains species, whilst *B.* (*L.*) *artigasi*, *B.* (*L.*) *cekalovici* and *B.* (*L.*) *negrei* seem to be more related to the Andean species of the subgenus *Leptosternus*.

RESUMEN. Notas sobre el género *Brachistosternus* (Scorpiones, Bothriuridae) en Chile, con la descripción de dos nuevas especies. En el presente artículo se describen dos nuevas especies del género *Brachistosternus* de la República de Chile. *Brachistosternus* (*Leptosternus*) *cekalovici* new species puede diferenciarse de la mayoría de las especies descriptas del género porque la glándula de la cara dorsal del telson, está dividida en dos mitades separadas. Las especies más relacionadas son *B.* (*L.*) *artigasi* Cekalovic 1974 y *B.* (*L.*) *negrei* Cekalovic 1975; en este trabajo se brindan también las redescripciones de ambas especies. *Brachistosternus cekalovici* sólo ha sido colectada en la localidad de Tres Cruces, en la provincia de Coquimbo, Chile. *Brachistosternus* (*Leptosternus*) *mattonii* n. sp se encuentra estrechamente relacionada con *B.* (*L.*) *donosoi* Cekalovic 1974, puede diferenciarse de ella por poseer un tegumento más granuloso, especialmente en la faz ventral del metasoma, por el mayor desarrollo de las espinas internas del hemiespermatóforo y por carecer de la glándula del telson. Tambien se brinda la redescripción de *B. donosoi*. Ambas especies se encuentran relacionadas con las especies argentinas de llanura, mientras que *B.* (*L.*) *artigasi*, *B.* (*L.*) *cekalovici* y *B.* (*L.*) *negrei* parecen estar más relacionadas con las especies andinas del subgénero *Leptosternus*.

Keywords: Scorpiones, *Brachistosternus*, new species, South America, biogeography, taxonomy

The genus *Brachistosternus* has been studied in Chile by Kraepelin (1911), Mello-Leitão (1941), Ochoa & Acosta (2002) and especially by Cekalovic (1970, 1973, 1974, 1975). There are records of this genus from Arica to Talca (Cekalovic 1974, 1975), but it is particularly diverse in northern and central Chile, the most arid regions of the country. Several specimens of *Brachistosternus* from this region were examined by the author, who recognized several unnamed species of the subgenus *Leptosternus*, most of them from coastal areas and high mountain habitats in the Andes. Both regions include environments that are slightly more humid than those found in the extremely xeric surrounding regions.

The species of *Brachistosternus* are always distributed in well-defined elevations; therefore the peculiar orography of Chile favors the presence of several different species within small geographic areas. A similar distributional pattern of the genus has been observed in northwestern Argentina (Ojanguren Affilastro 2002a).

Brachistosternus (*Leptosternus*) *cekalovici* new species and *Brachistosternus* (*Leptosternus*) *mattonii* new species are described here. In the first species the dorsal gland of the telson (Roig Alsina & Maury 1981) is divided

into separate halves. So far, only *Timogenes mapuche* Maury 1975, *T. sumatranus* Simon 1880 and some specimens of *B.* (*Leptosternus*) *negrei* Cekalovic 1975 share this characteristic within the family Bothriuridae (Maury 1975, 1982; De la Serna de Esteban 1977; Prendini 2000).

Brachistosternus cekalovici is very similar to *B.* (*L.*) *artigasi* Cekalovic 1974 and *B.* (*L.*) *negrei*. Although the original descriptions of *B. artigasi* and *B. negrei* given by Cekalovic (1974, 1975) are very complete, some characters currently used in the systematics of the genus remain undescribed; therefore the redescriptions of these species are provided.

Brachistosternus (*L.*) *mattonii* is described here and compared to the closely related species *B.* (*L.*) *donosoi* Cekalovic 1974. So far, this species has only been collected from coastal environments of northwestern Chile.

METHODS

The terminology of the hemispermatophores structures follows Maury (1974). Trichobothrial terminology follows Vachon (1974). Terminology of the telson gland follows Roig Alsina & Maury (1981). Terminology of the metasomal carinae follows Stahnke (1970). Abbreviations are as follows: MACN-Ar = Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", National Arachnological Collection (Cristina Scioscia); ARA = Arturo Roig Alsina personal collection; IADIZA = Instituto Argentino de Investigación de las Zonas Áridas (Sergio Roig Juñent); MZUC = Museo de Zoología de la Universidad de Concepción (Jorge Artigas); AMNH = American Museum of Natural History, New York, USA; AAOA = Andrés Alejandro Ojanguren Affilastro personal collection; FKPC = František Kovařík personal collection, Prague, Czech Republic. All measurements are given in mm and were taken using an ocular micrometer. Illustrations were produced using a stereomicroscope and camera lucida. The hemispermatophores were dissected from surrounding tissues and observed in 80% ethanol.

TAXONOMY

Family Bothriuridae Simon
Genus *Brachistosternus* Pocock
Brachistosternus* (*Leptosternus*) *cekalovici
new species
Figs. 1–13, 58

Type specimens.—Holotype male, CHILE: *Coquimbo Province*: Tres Cruces (29°22′24″S, 70°56′2″W), 10 January 1984, Maury (MACN-Ar 10243). Paratypes: CHILE: *Coquimbo Province*: Tres Cruces, 7 ♂, 4 ♀ and 2 juveniles, 10 January 1984, Maury (MACN-Ar 10244); 2 ♂ and 2 ♀, 10 January 1984, Maury (MZUC).

Other material examined.—CHILE: *Coquimbo Province*: Tres Cruces, 10 January 1984, 8 ♂, 6 ♀ and 3 juveniles, Roig Alsina (ARA).

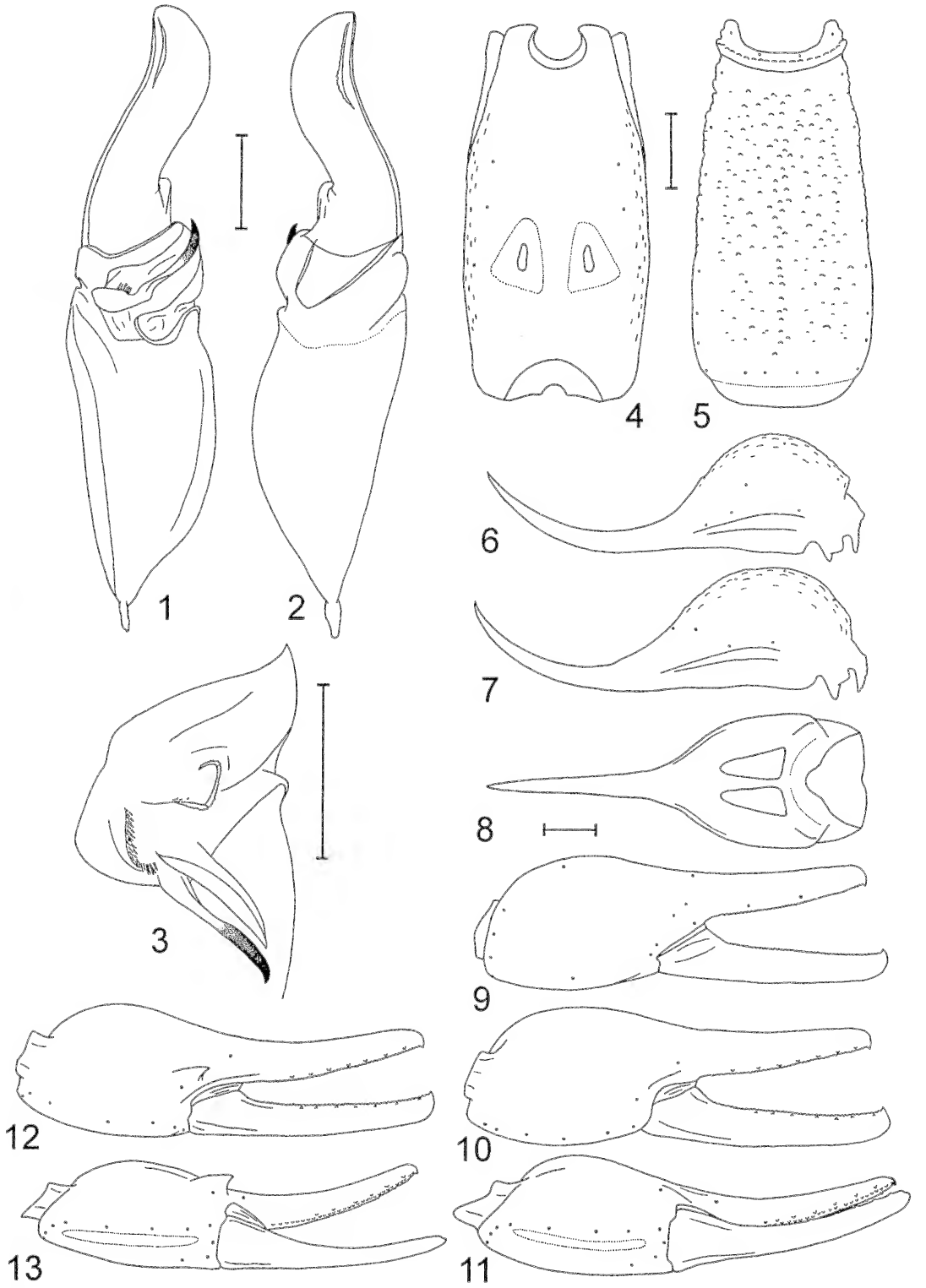
Etymology.—This species is named after the Chilean arachnologist Dr. Tomás Cekalovic Kuschevich.

Diagnosis.—*Brachistosternus* (*L.*) *cekalovici* can be distinguished from most other species of the genus because the dorsal gland of the telson is divided into separate halves (Fig. 8). Only some specimens of *B. negrei* share this characteristic (Fig. 53), but in most specimens of this species, this gland is absent. *Brachistosternus negrei* can be distinguished from *B. cekalovici* because it lacks the ventromedian carina of the fifth metasomal segment (Fig. 52) that is present in *B. cekalovici* (Fig. 5), and because it has two ventromedian stripes on metasomal segments II and III that are absent in *B. cekalovici*.

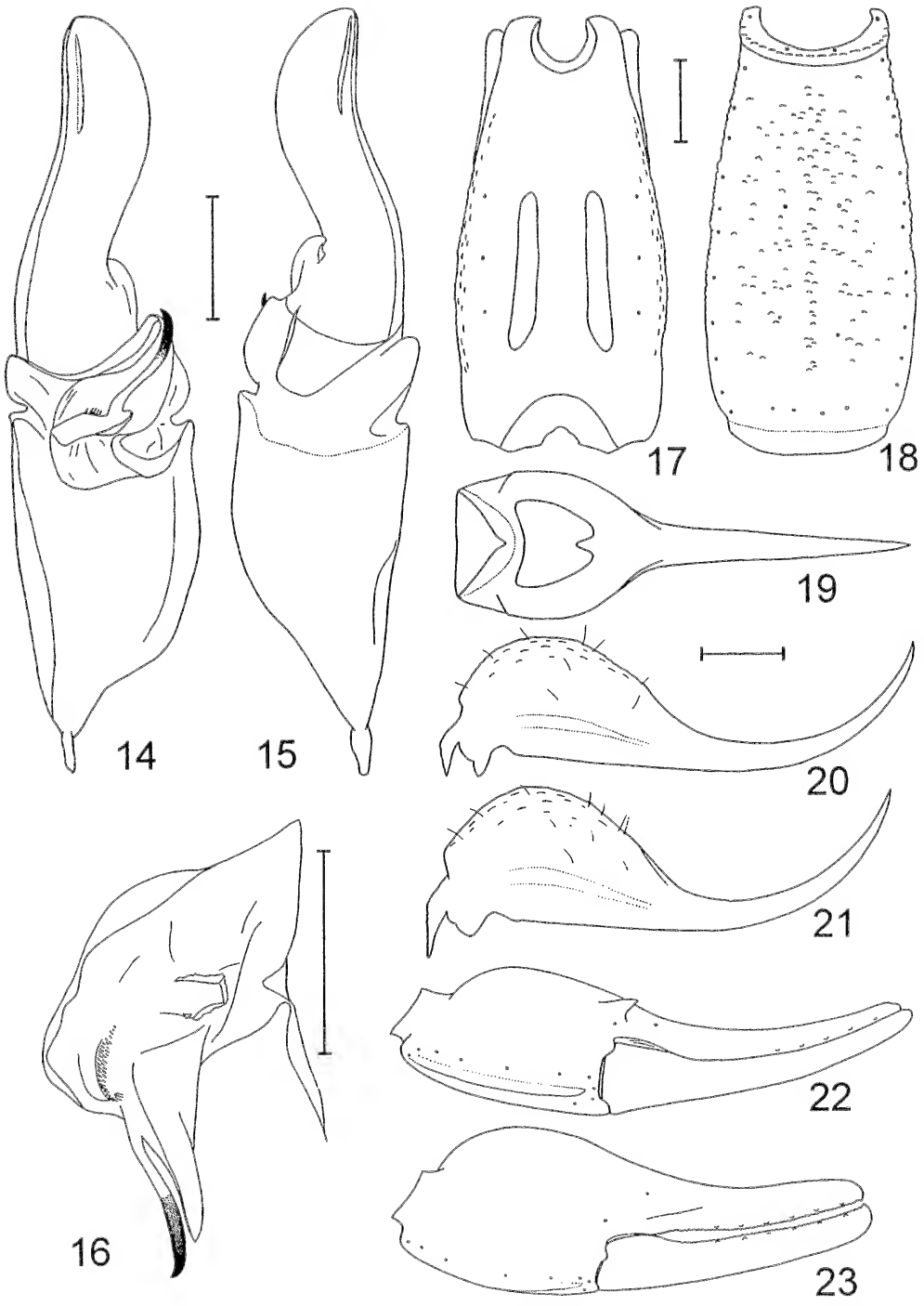
Brachistosternus cekalovici is most closely related to *B. artigasi*. Besides the shape of their telson glands (Figs. 8, 19) both species can be distinguished by the different shape of their caudal glands or androvestigia (Cekalovic 1973). In *B. artigasi* they occupy approximately 50% of the dorsal surface of the fifth metasomal segment (Fig. 17), whereas in *B. cekalovici* they occupy less than 25% (Fig. 4). *Brachistosternus* (*Leptosternus*) *galianoae*

→

Figures 1–13.—*Brachistosternus* (*Leptosternus*) *cekalovici*: 1. Left hemispermatophore, ventral aspect; 2. Left hemispermatophore, dorsal aspect; 3. Left hemispermatophore, detail of the lobe region; 4. Fifth metasomal segment, male, dorsal aspect; 5. Fifth metasomal segment, ventral aspect; 6. Telson, male, lateral aspect; 7. Telson, female, lateral aspect; 8. Telson, male, dorsal aspect. 9. Right pedipalpal chela,



female, retrolateral aspect; 10. Left pedipalpal chela, female, prolateral aspect; 11. Left pedipalpal chela, female, ventral aspect; 12. Left pedipalpal chela, male, prolateral aspect; 13. Left pedipalpal chela, male, ventral aspect. Scale bars = 1 mm.



Figures 14–23.—*Brachistosternus* (*Leptosternus*) *artigasi*: 14. Left hemispermatophore, ventral aspect; 15. Left hemispermatophore, dorsal aspect; 16. Left hemispermatophore, detail of the lobe region; 17. Fifth metasomal segment, male, dorsal aspect; 18. Fifth metasomal segment, ventral aspect; 19. Telson, male, dorsal aspect; 20. Telson, male, lateral aspect; 21. Telson, female, lateral aspect; 22. Left pedipalpal chela, male, ventral aspect; 23. Left pedipalpal chela, female, prolateral aspect. Scale bars = 1 mm.

Ojanguren Affilastro 2002, a species from Bolivia, also has such small caudal glands, but it has a single telson gland (Ojanguren Affilastro 2002b).

Description.—*Color:* General color dark yellow with a dusky pattern. Carapace with a dark stripe from the lateral ocelli to the postocular furrow; ocular tubercle black; the rest without pigmentation except for two posterolateral dark spots. Tergites with three spots, two lateral and a median spot, connected by a dark reticulated pigment. Sternites depigmented. Metasomal segments dorsally with two posterolateral dark spots and a median spot; segments I–III ventrally with two lateroventral stripes; IV with two lateroventral stripes and two median stripes that converge with the lateroventral stripes in the posterior margin of the segment; V with two lateroventral stripes and a median stripe that converge in the posterior margin of the segment where there is abundant reticulated pigmentation. Telson faintly spotted on the ventral surface. Legs with some spots on the prolateral sides of the femur and patella. Pedipalps: femur and patella with some spots on the retrolateral surface.

Morphology: Measurements of male holotype (MACN-Ar 10243) and a female paratype (MACN-Ar 10244) in Table 1. *Prosoma*: Chelicerae with two subdistal teeth in the movable finger; anterior edge of the carapace with a slight median bulge and six setae, two on each side and two in the middle; tegument slightly granular; anterior and posterior longitudinal sulcus, lateral sulcus and postocular furrow deeply marked; ocular tubercle medially situated on the carapace with a slight interocular sulcus, median ocelli two diameters apart with a seta behind each. *Sternum*: Sternum type 2 (Soleglad & Fet 2003), much wider than long; apex width equal to posterior width; posterior emargination quite well developed, with convex lateral lobes conspicuously separated. *Mesosoma*: Tergites I–VI smooth near the anterior margin and finely granular near the posterior margin; VII smooth medially, the rest densely granular, with two posterolateral carinae. *Metasoma*: Segment I: ventral surface smooth with three pairs of ventral setae, lateral surface with scattered granulation, dorsally smooth, dorsosubmedian, dorsolateral and median lateral carinae extend the entire length of the segment; segments II and III similar to segment I but less granular, with less well developed carinae and with four pairs of ventral setae; segment IV: dorsally smooth, lateral surfaces with sparse granulation, ventrally smooth with a large number of scattered setae; segment V: ventral surface irregularly granular, ventromedian and ventrolateral carinae extend the entire length of the segment (Fig. 5); dorsal and lateral surfaces finely granular or smooth; ventral setae usually comprising 4 rows: 1 basal row of 4 setae, and 3 posterior rows of 1 or 2 setae, in some specimens there is an additional row of 1 or 2 setae; in males the caudal glands occupy approximately 10 or 20% of the dorsal surface (Fig. 4). *Telson*: Sparsely granular; vesicle with rounded ventral surface; aculeus slightly curved, of the same length as the vesicle (Figs. 6 & 7); the dorsal gland of the telson is divided into two separated halves (Fig. 8), but in less than 10% of the examined specimens joined in the anterior margin. *Pedipalps*: Trichobothrial pattern, neobothriotaxic major type C: femur with 3 trichobothria: 1 *d,* 1 *i* and 1 *e*; patella with 3 ventral trichobothria, 2 dorsal trichobothria, 1 internal trichobothrium, and 13 external trichobothria: 3 *et,* 1 *est,* 2 *em,* 2 *esb* and 5 *eb*; chela with 27 trichobothria: 1 *Est,* 5 *Et,* 5 *v,* 1 *Esb,* 3 *Eb,* 1 *Dt,* 1 *Db,* 1 *et,* 1 *est,* 1 *esb,* 1 *eb,* 1 *dt,* 1 *dst,* 1 *dsb,* 1 *db,* 1 *ib,* 1 *it*; no intraspecific variation has been observed in these characters. Femur smooth, ventrointernal and dorsointernal carinae poorly developed, patella scarcely granular and without carinae; chela stout with relatively short fingers, smooth tegument, with a very developed ventroexternal carina (Figs. 9–13); in males the prolateral apophysis is well developed; movable finger with a central row of granules and 7 or 8 internal and external granules. *Legs*: finely granular; telotarsi I and II with the inner ungue 10–15% shorter than the external. *Hemispermatophore*: Distal lamina thick, slightly curved, and shorter than the basal portion (Figs. 1 & 2); cylindrical apophysis well developed, longer than the laminar apophysis; basal triangle well developed, formed by three or four crests (Fig. 3); internal spines absent; basal spines well developed; row of spines well developed, these spines can be branched in some specimens, and in some cases they can have up to three points.

Variation.—Total length in males, 50–55

Table 1.—Measurements (mm), number of pectinal teeth and telotarsal setae: *Brachistosternus cekalovici* new species, male holotype (MACN-Ar 10243) and female paratype (MACN-Ar 10244), and *Brachistosternus mattonii* new species, male holotype (MACN-Ar 10235) and female paratype (MACN-Ar 10236).

	Br. (L.) cekalovici		*Br. (L.) mattonii*	
	Male holotype	Female paratype	Male holotype	Female paratype
Total length	51.03	51.63	54.46	52.92
Carapace, length	5.66	6.92	5.74	6.14
Carapace, anterior width	4.20	4.44	3.88	4.53
Carapace, posterior width	6.38	6.71	6.3	6.87
Mesosoma, total length	13.86	13.53	14.83	15.75
Metasoma, total length	24.4	24.15	20.09	17.29
Metasomal segment I, length	3.72	4.36	4.61	4.04
Metasomal segment I, width	3.07	3.23	3.72	3.55
Metasomal segment I, height	3.96	4.04	2.83	2.83
Metasomal segment II, length	4.44	4.36	5.09	4.44
Metasomal segment II, width	3.15	3.15	3.31	3.07
Metasomal segment II, height	3.72	3.55	2.99	2.83
Metasomal segment III, length	4.85	4.36	5.09	4.61
Metasomal segment III, width	3.15	2.99	3.23	2.99
Metasomal segment III, height	3.47	3.31	2.67	2.51
Metasomal segment IV, length	5.33	5.01	5.74	5.25
Metasomal segment IV, width	2.91	2.75	2.99	2.83
Metasomal segment IV, height	3.23	3.07	2.54	2.34
Metasomal segment V, length	6.06	6.06	6.46	5.82
Metasomal segment V, width	2.51	2.42	3.23	2.82
Metasomal segment V, height	3.23	3.07	2.51	2.18
Telson, length	7.11	7.03	6.9	6.87
Vesicle, length	3.64	3.39	3.88	3.64
Vesicle, width	2.42	2.18	2.75	2.34
Vesicle, height	1.94	1.90	2.18	2.1
Aculeus, length	3.47	3.64	3.75	3.23
Pedipalp, total length	15.67	14.30	15.84	16.96
Femur, length	4.12	3.55	5.09	4.68
Femur, width	0.81	1.37	1.37	1.37
Patella, length	4.04	3.72	4.44	4.2
Patella, width	1.45	1.62	1.62	1.62
Chela, length	7.51	7.03	9.13	8.08
Chela, width	1.86	1.86	2.59	1.94
Chela, height	2.34	2.51	3.07	2.58
Movable finger, length	4.53	4.36	5.33	5.01
Fixed finger, length	4.01	3.87	4.9	4.72
Number of pectinal teeth, left-right	34-34	28-29	39-39	28-29
Telotarsus I, ventrointernal setae	3	3	4	3
Telotarsus I, ventroexternal setae	5	3	0	0
Telotarsus I, dorsal setae	10	9	8	8
Telotarsus II, ventrointernal setae	5	5	5	5
Telotarsus II, ventroexternal setae	5	3	4	4
Telotarsus II, dorsal setae	12	9	7	7
Telotarsus III, ventrointernal setae	9	9	7	7
Telotarsus III, ventroexternal setae	5	6	5	6
Telotarsus III, dorsal setae	13	12	10	10
Telotarsus IV, ventrointernal setae	6	5	4	5
Telotarsus IV, ventroexternal setae	4	5	4	5
Telotarsus IV, dorsal setae	6	6	5	4

mm (n = 15; mean = 52.9), 51–59 mm in females (n = 10; mean = 54.8). Length/width ratio of the fifth metasomal segment 1.81–2.22 (n = 10; mean = 2.01). Pectines with 33–36 pectinal teeth in males (n = 15; median = 35) and 28–32 in females (n = 10; median = 30). Length/height ratio of the pedipalpal chela 3.04–3.17 in males (n = 15; mean = 3.11) and 2.74–3.12 in females (n = 10; mean = 2.87). Telotarsus I with 3 or 4 ventrointernal setae (n = 20; median = 3), 3–5 ventroexternal setae (n = 20; median = 3) and 9 or 10 dorsal setae (n = 20; median = 10). Telotarsus II with 5 or 6 ventrointernal setae (n = 20; median = 5), 3 to 5 ventroexternal setae (n = 20; median = 3) and 9 to 12 dorsal setae (n = 20; median = 10). Telotarsus III with 8 or 9 ventrointernal setae (n = 25; median = 8), 5–7 ventroexternal setae (n = 25; median = 6) and 11–14 dorsal setae (n = 25; median = 12). Telotarsus IV with 5 or 6 ventrointernal setae (n = 25; median = 6), 4 or 5 ventroexternal setae (n = 25; median = 5) and 6 or 7 dorsal setae (n = 25; median = 6). Fourth metasomal segment with 31–38 ventral setae (n = 20; median = 36). Fifth metasomal segment with 9–12 ventrolateral setae (n = 25; median = 10), and 8–12 lateral setae (n = 25; median = 9).

Distribution.—This species has only been collected at the type locality (Fig. 58).

Brachistosternus* (*Leptosternus*) *mattonii
new species
Figs. 24–35, 41, 58

Type specimens.—Holotype male, CHILE: *Antofagasta Province*: Hornitos (22°55′S, 70°18′W), 2 October 1983, Maury (MACN-Ar 10235). Paratypes: CHILE: *Antofagasta Province*: Antofagasta (23°39′S, 70°24′W), 1 ♀, 22 October 1982, Maury (MACN-Ar 10236); Hornitos, 1 ♂, 6 October 1983, Roig Alsina (MACN-Ar 10245). *Iquique Province*: Alto Patache (20°45′S, 70°9′W), 1 juvenile ♂, 26 August 1998, C. Moreira (FKPC).

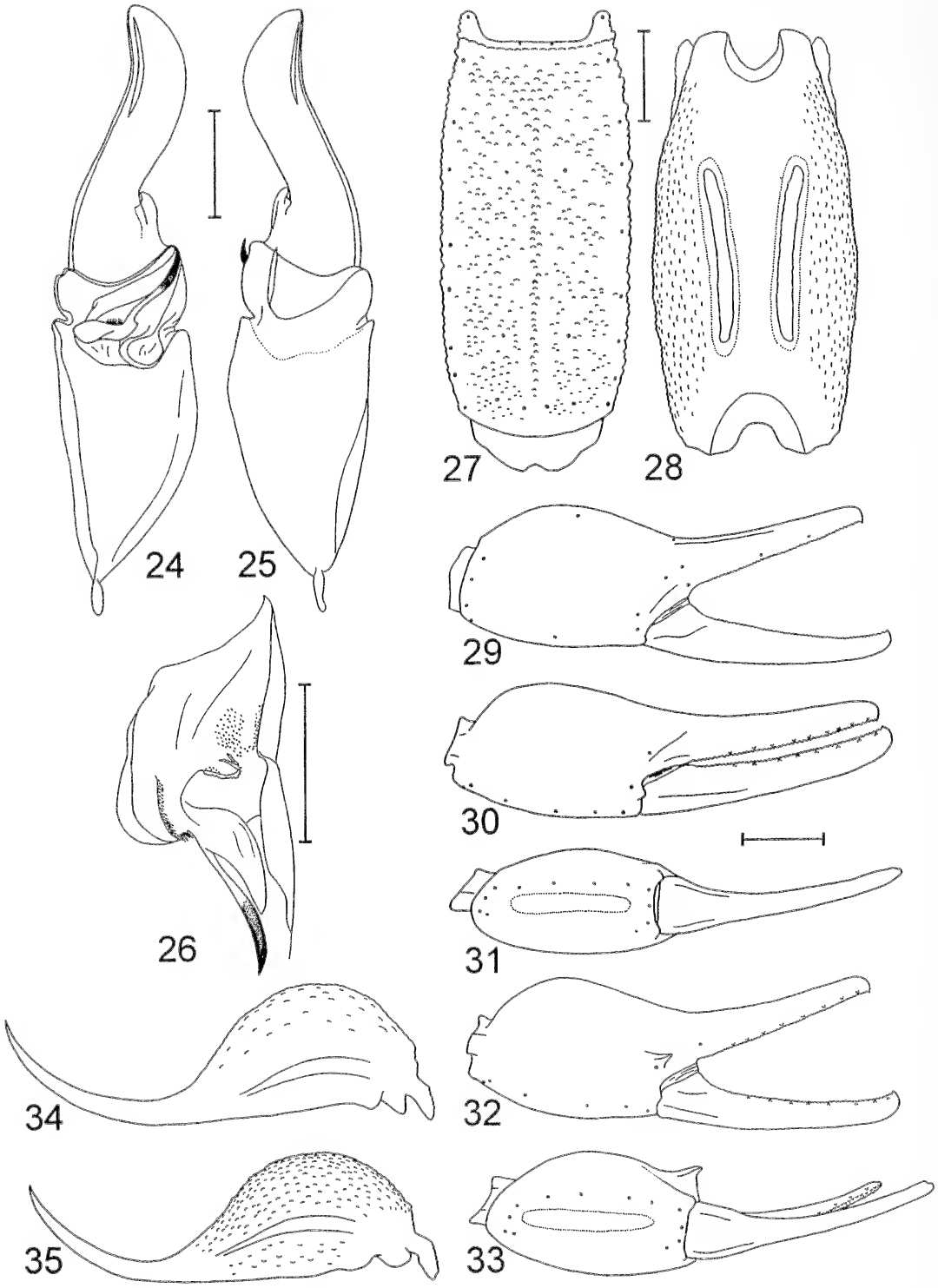
Other material examined.—CHILE: *Antofagasta Province*: Hornitos, 6 October 1983, 2 ♂ and 2 juveniles, Roig Alsina (ARA).

Etymology.—This species is named after the Argentinian arachnologist Camilo Iván Mattoni.

Diagnosis.—*Brachistosternus* (*L.*) *mattonii* is most closely related to *B.* (*L.*) *donosoi*, from which it can be distinguished by its more densely granular tegument, especially on the ventral surface of the metasomal segments (Figs. 41, 42); the lack of a telson gland; and the lower number of ventral setae on metasomal segment V (6–9 in *B. mattonii* vs. 14–19 in *B. donosoi*). There are also minor differences in the shape of the hemispermatophore (Figs. 24–26, 36–38), especially in the development of the internal spines. In *B. mattonii* they are distributed in two areas, one above the basal triangle and the other in front of it (Fig. 26), with a smooth area in the middle; whereas in *B. donosoi* the internal spines are restricted to a small area in front of the basal triangle (Fig. 38). In the rest of the species of the genus, these spines usually occupy the whole area above the basal triangle (Ojanguren Affilastro & Roig Alsina 2001) or they are absent, as in the Andean species of the subgenus *Leptosternus* (Roig Alsina 1977; Ochoa & Acosta 2002).

Description.—*Color:* Yellow with some spots on the carapace and the tergites. Carapace with a dark stripe from the lateral ocelli to the postocular furrow; ocular tubercle black; the rest lacking pigmentation. Tergites with three spots, two lateral and one median that join in some specimens. Sternites, metasomal segments, telson, pedipalps, and pectines unpigmented. Some specimens are almost completely unpigmented.

Morphology: Measurements of male holotype (MACN-Ar 10235) and female paratype (MACN-Ar 10236) in Table 1. *Prosoma*: Chelicerae with two subdistal teeth in the movable finger; anterior edge of the carapace with a slight median bulge and four setae, one on each side and two in the middle; tegument densely granular; anterior and posterior longitudinal sulcus, lateral sulcus and postocular furrow deeply marked; ocular tubercle in the middle of the carapace with a slight interocular sulcus, median ocelli two diameters apart with a seta behind each. *Sternum*: Sternum type 2 (Soleglad & Fet 2003), much wider than long; apex width equal to posterior width; posterior emargination quite well developed, with convexed lateral lobes conspicuously separated. *Mesosoma*: Tergites I–VI finely granular near the anterior margin and densely granular near the posterior margin; VII finely granular medially, the rest densely granular, with two posterolateral carinae. *Metasoma*: segments I–III: ventral and lateral



Figures 24–35.—*Brachistosternus* (*Leptosternus*) *mattonii*: 24. Left hemispermatophore, ventral aspect; 25. Left hemispermatophore, dorsal aspect; 26. Left hemispermatophore, detail of the lobe region; 27. Fifth metasomal segment, male, ventral aspect; 28. Fifth metasomal segment, dorsal aspect; 29. Right pedipalpal chela, female, retrolateral aspect; 30. Left pedipalpal chela, female, prolateral aspect; 31. Left pedipalpal chela, female, ventral aspect; 32. Left pedipalpal chela, male, prolateral aspect; 33. Left pedipalpal chela, male, ventral aspect; 34. Telson, female, lateral aspect; 35. Telson, male, lateral aspect. Scale bars = 1 mm.

surfaces densely granular, dorsally finely granular, dorsosubmedian, dorsolateral and median lateral carinae extend the entire length of the segment; segment IV: dorsally finely granular, lateral surfaces densely granular, ventrally densely granular with a large number of scattered setae, each one in a depression with smooth tegument (Fig. 41); segment V: ventral surface irregularly granular, ventromedian and ventrolateral carinae extend the entire length of the segment; dorsal and lateral surfaces finely granular or smooth; ventral setae usually comprising 3 rows (Fig. 27): 1 basal row of 2–4 setae, and 2 posterior rows of 1 or 2 setae, in one specimen there is an additional row of 2 setae; in males the caudal glands are long and narrow (Fig. 28). The juveniles and the females of the species are less granular than males. *Telson*: Densely granular in males (Fig. 35) and with scarce granulation in females (Fig. 34); vesicle with rounded ventral surface; aculeus slightly curved, of the same length as the vesicle; in males the telson gland is absent, but there is a small circular depression on the dorsal surface of the vesicle. *Pedipalps*: Trichobothrial pattern, neobothriotaxic major type C: femur with 3 trichobothria: 1 *d,* 1 *i* and 1 *e*; patella with 3 ventral trichobothria, 2 dorsal trichobothria, 1 internal trichobothrium, and 13 external trichobothria: 3 *et,* 1 *est,* 2 *em,* 2 *esb* and 5 *eb*; chela with 27 trichobothria: 1 *Est,* 5 *Et,* 5 *v,* 1 *Esb,* 3 *Eb,* 1 *Dt,* 1 *Db,* 1 *et,* 1 *est,* 1 *esb,* 1 *eb,* 1 *dt,* 1 *dst,* 1 *dsb,* 1 *db,* 1 *ib,* 1 *it*; no intraspecific variation has been observed in these characters. Femur scarcely granular, ventrointernal, ventroexternal, and dorsointernal carinae well developed, patella scarcely granular; ventrointernal and ventroexternal carinae well developed; chela stout with long fingers, tegument finely granular or smooth, with a very well developed ventrointernal carina (Figs. 29–33); in males the prolateral apophysis is well developed; movable finger with a central row of granules and 7 or 8 internal and external granules. *Legs*: Finely granular; telotarsi I and II with the inner ungue 5 to 10% shorter than the external one. *Hemispermatophore*: Distal lamina thick, slightly curved, approximately the same size as the basal portion (Figs. 24 & 25); cylindrical apophysis well developed, longer than the laminar apophysis; basal triangle well developed, formed by three or four crests (Fig. 26); internal spines distributed in two areas, one above the basal triangle and the other in front of it; basal spines well developed; row of spines well developed, these spines can be ramified in some specimens.

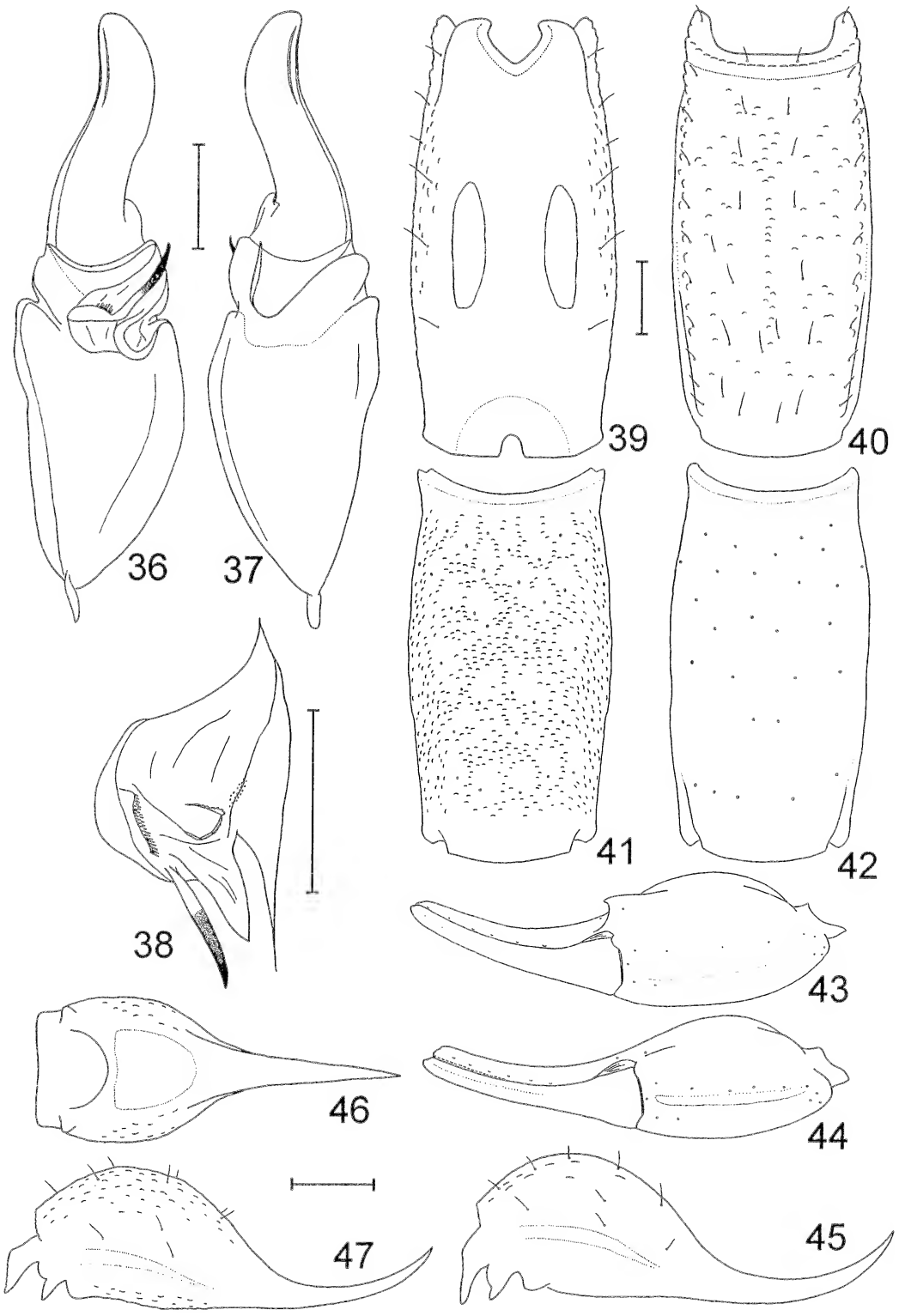
Variation.—Total length in males, 49–58 mm (n = 4; mean = 54.25) and 53 mm in the only studied female. Pectines with 36–41 pectinal teeth in males (n = 4, median = 39) and 28–29 in the only studied female. Length/width ratio of the fifth metasomal segment 2 to 2.11 in males (n = 4; mean = 2.06) and 2.05 in the only studied female. Length/height ratio of the pedipalpal chela 2.90–3.11 in males (n = 4; mean = 2.98) and 3.13 in the only studied female. Telotarsus I with 3 or 4 ventrointernal setae (n = 8; median = 3), and 7 or 8 dorsal setae (n = 8; median = 8), no ventroexternal setae have been observed. Telotarsus II with 3–5 ventrointernal setae (n = 8; median = 4), 3–5 ventroexternal setae (n = 8; median = 4) and 7–9 dorsal setae (n = 8; median = 7). Telotarsus III with 6 or 7 ventrointernal setae (n = 8; median = 7), 4–6 ventroexternal setae (n = 8; median = 6) and 9–11 dorsal setae (n = 8; median = 10). Basitarsus III with 7 or 8 dorsal setae (n = 8; median = 7). Telotarsus IV with 4 or 5 ventrointernal setae (n = 8; median = 5), 4 or 5 ventroexternal setae (n = 8; median = 5) and 4–6 dorsal setae (n = 8; median = 6). Fourth metasomal segment with 28–36 ventral setae (n = 7; median = 34). Fifth metasomal segment with 8 ventrolateral setae (n = 8), and 8 or 9 lateral setae (n = 7; median = 8).

Distribution.—This species has only been collected at three coastal localities in northern Chile: Hornitos and Antofagasta, both in Antofagasta Province; and Alto Patache, in Iquique Province (Fig. 58). Northerly, in coastal areas of southern Peru, this species is replaced by *B.* (*L.*) *turpuq* Ochoa 2002 (Ochoa 2002); southerly, in central Chile *B. mattonii* is replaced by *B.* (*L.*) *roigalsinai* Ojanguren Affilastro 2003 and *B.* (*L.*) *sciosciae* Ojanguren Affilastro 2003 (Ojanguren Affilastro 2003).

Brachistosternus (*Leptosternus*) *donosoi*
Cekalovic 1974
Figs. 36–40, 42–47, 58

Brachistosternus (*Leptosternus*) *donosoi* Cekalovic 1974: 250–252.

Type material.—Holotype male, CHILE, *Tarapaca Province,* Pampa del Tamarugal, 10



Figures 36–47.—36–40, 42–47. *Brachistosternus* (*Leptosternus*) *donosoi*: 36. Left hemispermatophore, ventral aspect; 37. Left hemispermatophore, dorsal aspect; 38. Left hemispermatophore, detail of the lobe region; 39. Fifth metasomal segment, male, dorsal aspect; 40. Fifth metasomal segment, ventral aspect; 42. Fourth metasomal segment, male, ventral aspect; 43. Right pedipalpal chela, male, ventral aspect; 44.

km E Pica (20°30′S, 69°21′W) (MZUC 530, not examined).

Description.—*Color:* Yellow with some spots on the carapace and the tergites. Carapace with a dark stripe from the lateral ocelli to the postocular furrow; ocular tubercle black; the rest lacking pigmentation. Tergites with two faint lateral spots. Sternites, metasomal segments, telson, pedipalps, and pectines unpigmented. Some specimens are almost completely unpigmented.

Morphology: Measurements a of a male specimen (AAOA) and female specimen (AMNH) in Table 2. *Prosoma*: Chelicerae with two subdistal teeth in the movable finger; anterior edge of the carapace with a slight median bulge, tegument densely granular; anterior and posterior longitudinal sulcus, lateral sulcus and postocular furrow deeply marked; ocular tubercle in the middle of the carapace with a slight interocular sulcus, median ocelli two diameters apart with a seta behind each. *Sternum*: Sternum type 2 (Soleglad & Fet 2003), much wider than long; apex width equal to posterior width; posterior emargination quite well developed, with convexed lateral lobes conspicuously separated. *Mesosoma*: Tergites: I–VI finely granular near the anterior margin and finely granular near the posterior margin in males, smooth in females; VII densely granular, with two posterolateral carinae. *Metasoma*: Segments I–III: ventral and lateral surfaces densely granular, dorsally finely granular, dorsosubmedian, dorsolateral and median lateral carinae extend the entire length of the segment; segment IV: dorsally finely granular, lateral surfaces densely granular, ventrally smooth with a large number of scattered setae (Fig. 42); segment V: ventral surface smooth near the anterior margin and irregularly granular in the second half, the ventromedian carina is weakly developed or absent and the ventrolateral carinae extend throughout the entire length of the segment (Fig. 40); the ventral setae usually comprise 5 rows: 2 basal rows of 4–6 setae and 3 or 4 posterior rows of 2–4 setae; dorsal and lateral surfaces finely granular or smooth; in males, the caudal glands occupy more than 60% of the dorsal surface (Fig. 39). *Telson*: Densely granular in males (Fig. 47) and with scarce granulation in females (Fig. 45); vesicle with rounded ventral surface; aculeus slightly curved, of the same length as the vesicle; in males the telson gland is almost triangular (Fig. 46). *Pedipalps*: Trichobothrial pattern, neobothriotaxic major type C: femur with 3 trichobothria: 1 *d,* 1 *i* and 1 *e*; patella with 3 ventral trichobothria, 2 dorsal trichobothria, 1 internal trichobothrium, and 13 external trichobothria: 3 *et,* 1 *est,* 2 *em,* 2 *esb* and 5 *eb*; chela with 27 trichobothria: 1 *Est,* 5 *Et,* 5 *v,* 1 *Esb,* 3 *Eb,* 1 *Dt,* 1 *Db,* 1 *et,* 1 *est,* 1 *esb,* 1 *eb,* 1 *dt,* 1 *dst,* 1 *dsb,* 1 *db,* 1 *ib,* 1 *it*; no intraspecific variation has been observed in these characters. Femur scarcely granular, ventrointernal, ventroexternal, and dorsointernal carinae well developed, patella scarcely granular; ventrointernal and ventroexternal carinae well developed; chela stout with long fingers, tegument finely granular or smooth, with a very well developed ventrointernal carina (Figs. 43 & 44); in males the prolateral apophysis is well developed; movable finger with a central row of granules and 7 or 8 internal and external granules. *Legs*: Finely granular; telotarsi I and II with the inner ungue 10–15% shorter than the external one. *Hemispermatophore*: Distal lamina thick and of the same proportions as the basal portion (Figs. 36 & 37); cylindrical apophysis well developed, and longer than the laminar apophysis; basal triangle well developed formed by three or four crests; internal spines poorly developed reduced to a small area in front of the basal triangle (Fig. 38); basal spines well developed; row of spines well developed.

Variation.—Total length in males, 56–64 mm (n = 8; mean = 59.5), 53–62 mm in females (n = 9; mean = 59.20). Pectines with 28–33 teeth in males (n = 6; median = 32), 25–31 in females (n = 9; median = 29). Length/width ratio of the fifth metasomal segment 2.10–2.57 in males (n = 5; mean = 2.34), 1.95–2.35 in females (n = 5; mean = 2.21). Length/height ratio of the pedipalpal

←

Right pedipalpal chela, female, ventral aspect; 45. Telson, female, lateral aspect; 46. Telson, male, dorsal aspect; 47. Telson, male, lateral aspect. 41. *Brachistosternus* (*L.*) *mattonii*, fourth metasomal segment, male, ventral aspect. Scale bars = 1 mm.

Table 2.—Measurements (mm), number of pectinal teeth and telotarsal setae: of a male specimen and a female specimen of *Brachistosternus artigasi*, *B. donosoi* and *B. negrei*.

	Br. (L.) artigasi		*Br. (L.) donosoi*		*Br. (L.) negrei*	
	Male (ARA)	Female (AMNH)	Male (AAOA)	Female (AMNH)	Male (MACN)	Female (MACN)
Total length	53.81	55.22	56.27	59.07	55.78	65.37
Carapace, length	6.2	6.53	6.65	7.32	6.54	7.76
Carapace, anterior width	3.87	4.13	4.26	4.66	4.68	6.06
Carapace, posterior width	5.8	6.33	6.92	7.45	6.7	8.65
Mesosoma, total length	17.42	18.62	15.96	17.02	14.67	18.75
Metasoma, total length	23.59	24.07	26.34	27.41	34.57	38.86
Metasomal segment I, length	3.6	4	3.99	4.66	4.04	4.44
Metasomal segment I, width	4.13	3.93	4.12	4.66	4.44	5.41
Metasomal segment I, height	3.4	3.2	3.33	3.72	3.39	4.04
Metasomal segment II, length	4.33	4.47	4.66	4.92	4.84	5.66
Metasomal segment II, width	3.87	3.6	3.72	3.99	4.28	4.12
Metasomal segment II, height	3.2	3.13	3.33	3.59	3.55	4.04
Metasomal segment III, length	4.33	4.47	5.32	5.19	5.25	5.66
Metasomal segment III, width	3.67	3.47	3.59	3.72	4.04	4.68
Metasomal segment III, height	3.13	3	3.19	3.46	3.55	4.04
Metasomal segment IV, length	5.33	5.13	5.99	5.99	6.06	6.46
Metasomal segment IV, width	3.53	3.2	3.33	3.46	3.88	4.61
Metasomal segment IV, height	2.8	2.67	2.93	3.19	3.31	3.96
Metasomal segment V, length	6	6	6.38	6.65	4.68	8.08
Metasomal segment V, width	3.47	3.13	3.33	3.33	2.02	4.44
Metasomal segment V, height	2.6	2.33	2.79	2.79	1.69	3.64
Telson, length	6.6	6	7.32	7.32	7.27	8.56
Vesicle, length	3	2.67	3.99	3.99	3.23	4.2
Vesicle, width	2.07	2.07	2.79	3.1	2.83	3.23
Vesicle, height	1.87	1.87	2.39	2.45	2.18	2.83
Aculeus, length	3.6	3.33	3.33	3.33	4.04	4.36
Pedipalp, total length	15.38	14.52	20.57	18.75	17.12	18.75
Femur, length	4	3.67	5.94	4.92	4.44	4.85
Femur, width	1.33	1.47	1.73	1.73	1.86	1.69
Patella, length	3.93	3.67	5.05	5.05	4.44	4.85
Patella, width	1.8	1.73	1.86	2.13	1.94	2.26
Chela, length	7.45	7.18	9.58	8.78	8.24	9.05
Chela, width	1.73	1.86	2.66	2.53	2.42	2.34
Chela, height	2.39	2.66	3.33	3.06	3.23	3.07
Movable finger, length	4.52	4.39	5.32	4.79	4.85	5.41
Fixed finger, length	3.99	3.99	4.92	4.52	4.2	4.98
Number of pectinal teeth, left-right	30-29	24-24	31-31	27-27	34-34	31-31
Telotarsus I, ventrointernal setae	3	3	3	3	2	2
Telotarsus I, ventroexternal setae	7	6	0	0	0	0
Telotarsus I, dorsal setae	9	9	7	8	7	8
Telotarsus II, ventrointernal setae	4	5	5	5	4	4
Telotarsus II, ventroexternal setae	4	4	4	3	2	1
Telotarsus II, dorsal setae	11	11	8	9	8	9
Telotarsus III, ventrointernal setae	11	12	8	8	6	6
Telotarsus III, ventroexternal setae	5	4	5	5	4	2
Telotarsus III, dorsal setae	11	11	12	11	6	5
Telotarsus IV, ventrointernal setae	4	5	5	5	4	5
Telotarsus IV, ventroexternal setae	5	5	5	5	4	4
Telotarsus IV, dorsal setae	6	5	5	6	5	5

chela 2.87–2.97 in males (n = 5; mean = 2.91), 2.85–3.15 in females (n = 5; mean = 3.03). Telotarsus I with 3 or 4 ventrointernal setae (n = 10; median = 3), 0 or 1 ventroexternal setae (n = 10; median = 0) and 7 or 8 dorsal setae (n = 10; median = 7). Telotarsus II with 4 or 5 ventrointernal setae (n = 10; median = 5), 3 or 4 ventroexternal setae (n = 10; median = 4) and 7–10 dorsal setae (n = 10; median = 9). Telotarsus III with 6–8 ventrointernal setae (n = 10; median = 8), 5 or 6 ventroexternal setae (n = 10; median = 5) and 11–13 dorsal setae (n = 10; median = 12). Telotarsus IV with 4 or 5 ventrointernal setae (n = 10; median = 5), 4 or 5 ventroexternal setae (n = 10; median = 5) and 5 or 6 dorsal setae (n = 10; median = 6). Fourth metasomal segment with 26–32 ventral setae (n = 10). Fifth metasomal segment with 9 or 10 ventrolateral setae (n = 10; median = 10), and 6 or 7 lateral setae (n = 10; median = 6).

Distribution.—This species has been collected from 800–1400 m a.s.l. at Tarapacá province, in northern Chile (Fig. 58). Most of the localities where this species has been collected are placed at the "Pampa del Tamarugal"; and are related with forests of *Prosopis tamarugo* Philippi. This species was not found by the author in coastal areas of this province.

Material examined.—CHILE: *Tarapaca Province*: Fuerte Baquedano (20°11′S, 69°47′W), 26 December 1977, 2 ♂, 4 ♀ and 2 juveniles, Peña (AMNH); December 1978, 2 ♂, 6 ♀ and 7 juveniles, Peña (AMNH); Quebrada de Tarapaca (19°40′S, 69°10′W), 25 January 1992, 1 ♀ and 3 juveniles, Peña (AMNH); Dolores (19°40′S 69°57′W), 8 February 1992, 1 juvenile, Peña (AMNH); 25 Km. West Pica (20°31′S, 69°22′W), 6 December 2001, 1 ♂ and 1 juvenile, Ojanguren Affilastro & Korob (AAOA).

Brachistosternus (*Leptosternus*) *artigasi*
Cekalovic 1974
Figs. 14–23, 58

Brachistosternus (*Leptosternus*) *artigasi* Cekalovic 1974: 248–250.

Type material.—Holotype male, CHILE, *Coquimbo Province,* La Serena, Lomas de Peñuelas (29°54′S, 71°15′W) (MZUC 528, examined).

Description.—*Color:* General color dark yellow with a dusky pattern. Carapace with a dark stripe from the lateral ocelli to the postocular furrow; ocular tubercle black; the rest without pigmentation except for two posterolateral dark spots. Tergites with three spots, two lateral and a median spot, connected by a dark reticulated pigment. Sternites depigmented. Metasomal segments dorsally with two posterolateral dark spots and a median spot, connected by a dark reticulated pigment; segments I to III ventrally with two lateroventral stripes; IV with two lateroventral stripes and a thin median stripe, that converge with the lateroventral stripes in the posterior margin of the segment; V with two lateroventral stripes and a median stripe that converge in the posterior margin of the segment where there is abundant reticulated pigmentation. Telson faintly spotted on the ventral surface. Legs with some spots on the prolateral sides of the femur and patella. Pedipalps: femur, patella and chella with some spots on the retrolateral surface.

Morphology: Measurements a of a male specimen (ARA) and female specimen (AMNH) in Table 2. *Prosoma*: Chelicerae with two subdistal teeth in the movable finger; anterior edge of the carapace with a slight median bulge; tegument densely granular; anterior longitudinal sulcus slightly marked; posterior longitudinal sulcus, lateral sulcus and postocular furrow deeply marked; ocular tubercle medially situated on the carapace with a slight interocular sulcus, median ocelli two diameters apart with a seta behind each. *Sternum*: Sternum type 2 (Soleglad & Fet 2003), much wider than long; apex width equal to posterior width; posterior emargination quite well developed, with convexed lateral lobes conspicuously separated. *Mesosoma*: Tergites I to VI smooth near the anterior margin and finely granular near the posterior margin; VII densely granular, with two posterolateral carinae. *Metasoma*: Segment I: ventral surface smooth, lateral surface finely granular, dorsally smooth, dorsosubmedian, dorsolateral and median lateral carinae slightly marked, extend the entire length of the segment; segments II and III similar to segment I but less granular, with less well developed carinae; segment IV: dorsally smooth, lateral surfaces with sparse granulation, ventrally smooth with a large number of scattered setae; segment V: ventral surface irregularly granular, the ventromedian and ventrolateral carinae extend throughout the entire length of the seg-

ment (Fig. 18); the ventral setae usually comprise 3 rows: 1 basal row of 2–5 setae, 1 median row of 1 or 2 setae, and 1 posterior row of 1 or 2 setae; dorsal and lateral surfaces finely granular or smooth; in males, the caudal glands occupy approximately 50% of the dorsal surface (Fig. 17). *Telson*: Sparsely granular; vesicle with rounded ventral surface; aculeus slightly curved, slightly longer than the vesicle (Figs. 20 & 21); the dorsal gland of the telson is almost triangular, and in most specimens the posterior corner of this triangle is doubled (Fig. 19). *Pedipalps*: Trichobothrial pattern, neobothriotaxic major type C: femur with 3 trichobothria: 1 *d*, 1 *i* and 1 *e*; patella with 3 ventral trichobothria, 2 dorsal trichobothria, 1 internal trichobothrium, and 13 external trichobothria: 3 *et*, 1 *est*, 2 *em*, 2 *esb* and 5 *eb*; chela with 27 trichobothria: 1 *Est*, 5 *Et*, 5 *v*, 1 *Esb*, 3 *Eb*, 1 *Dt*, 1 *Db*, 1 *et*, 1 *est*, 1 *esb*, 1 *eb*, 1 *dt*, 1 *dst*, 1 *dsb*, 1 *db*, 1 *ib*, 1 *it*; no intraspecific variation has been observed in these characters. Femur smooth, ventrointernal and dorsointernal carinae poorly developed, patella scarcely granular and without carinae; chela stout with relatively short fingers, smooth tegument, with a very developed ventroexternal carina (Figs. 22 & 23); in males the prolateral apophysis is well developed; movable finger with a central row of granules and 7 or 8 internal and external granules. *Legs*: Smooth in females and finely granular in males; The inner ungue of telotarsi I and II are 5–10% shorter than the external one. *Hemispermatophore*: Distal lamina thick and shorter than the basal portion (Figs. 14 & 15); cylindrical apophysis well developed, and longer than the laminar apophysis; basal triangle well developed formed by three or four crests (Fig. 16); internal spines absent; basal spines well developed; row of spines well developed.

Variation.—Total length in males, 49–60 mm (n = 10; mean = 53.9); 47–57 in females (n = 6; mean = 50.8). Pectines with 25–31 pectinal teeth in males (n = 11; median = 27); 22–29 in females (n = 6; median = 25). Length/height ratio of the pedipalpal chela 3.00–3.23 in males (n = 11; mean = 3.11); 2.75–2.91 in females (n = 6; mean = 2.87). Telotarsus I with 3 or 4 ventrointernal setae (n = 10; median = 3), 6–8 ventroexternal setae (n = 10; median = 6) and 9 or 10 dorsal setae (n = 10; median = 9). Telotarsus II with 3–5 ventrointernal setae (n = 10; median = 5), 4–6 ventroexternal setae (n = 10; median = 4) and 10 or 11 dorsal setae (n = 10; median = 11). Telotarsus III with 10–13 ventrointernal setae (n = 10; median = 12), 5–7 ventroexternal setae (n = 10; median = 7) and 12–15 dorsal setae (n = 10; median = 15). Telotarsus IV with 4 or 5 ventrointernal setae (n = 10; median = 5), 4 or 5 ventroexternal setae (n = 10; median = 5) and 5–7 dorsal setae (n = 10; median = 5). Fourth metasomal segment with 30–35 ventral setae (n = 5). Fifth metasomal segment with 9–13 ventrolateral setae (n = 11; median = 12), and 9–13 lateral setae (n = 5; median = 11). Length/width ratio of the fifth metasomal segment 2–2.26 (n = 11; mean = 2.15).

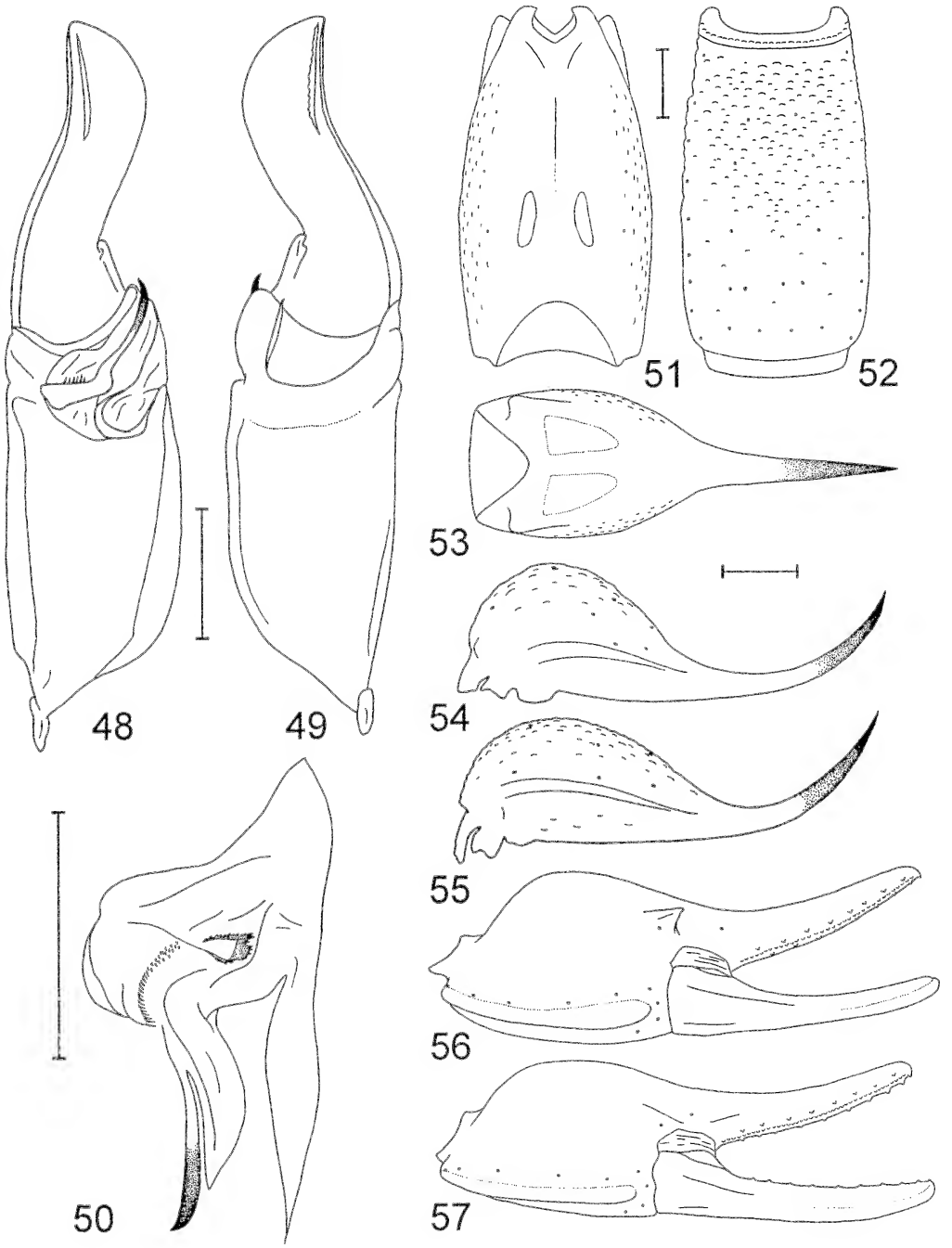
Distribution.—Besides the type locality at Lomas de Peñuelas, La Serena, this species has only been collected in other neighboring localities: Guanaqueras, 2, 10 and 20 km south of Coquimbo. All of these localities belong to the Coquimbo Province, and are very close to the coast (Fig. 58). At this latitude, only a few kilometers inland this species is replaced by *B. cekalovici*. The author failed to collect this species at Pan de Azúcar National Park and Caldera, both in Copiapó Province; where inhabits *B.* (*L.*) *sciosciae* (Ojanguren Affilastro 2003).

Material examined.—CHILE: *Coquimbo Province*: Holotype male, La Serena, Lomas de Peñuelas (29°54′S, 71°15′W), 5 September 1968, Cekalovic (MZUC 528); Guanaqueras (30°11′60″S, 71°25′60″W), 9 January 1984, 1 ♂, Roig Alsina (ARA); 25 November 1992, 1 ♂, Roig Juñent (IADIZA); 9 January 1984, 1 ♂, Maury (MACN-Ar); 10 km S Coquimbo (30°4′S, 71°22′30″W), 2 November 1983, 1 juvenile, Maury (MACN-Ar); 20 km. S. Coquimbo, 1 January, 1985, 13 juveniles, 8 ♂ and 10 ♀, Platnick & Francke (AMNH); 2 km S Coquimbo, 1 January 1985, 2 ♂ and 3 juveniles, Platnick & Francke (AMNH).

Brachistosternus (*Leptosternus*) *negrei* Cekalovic 1975
Figs. 48–58

Brachistosternus (*Leptosternus*) *negrei* Cekalovic 1975: 69–72.

Type material.—Holotype male, CHILE, *Talca Province*, 22 miles N of Talca (35°17′S, 71°38′W) (MZUC 546, not examined). The holotype of this species is lost, but the author



Figures 48–57.—*Brachistosternus* (*Leptosternus*) *negrei*: 48. Left hemispermatophore, ventral aspect; 49. Left hemispermatophore, dorsal aspect; 50. Left hemispermatophore, detail of the lobe region; 51. Fifth metasomal segment, male, dorsal aspect; 52. Fifth metasomal segment, ventral aspect; 53. Telson, male, dorsal aspect; 54. Telson, female, lateral aspect; 55. Telson, male, lateral aspect; 56. Left pedipalpal chela, male, ventral aspect; 57. Left pedipalpal chela, female, ventral aspect. Scale bars = 1 mm.

was able to study one male specimen identified by Cekalovic as *B. negrei*.

Description.—*Color:* General color dark yellow with a dusky pattern. Carapace with a dark stripe from the lateral ocelli to the postocular furrow; ocular tubercle black; anterior edge of the carapace with dark spots; the rest without pigmentation except for two posterolateral dark spots. Tergites with two lateral spots, and a median clear stripe without pigmentation. Sternites depigmented. Metasomal segments dorsally with two posterolateral dark spots and a median spot; segments I–IV ventrally with two lateroventral stripes and two median stripes, in some specimens the median stripes can be absent; V with two lateroventral stripes and a median stripe, in some specimens the median stripe can be absent, but in very pigmented specimens there are three median stripes. Telson faintly spotted on the ventral surface. Legs with some spots on femur and patella. Pedipalps: femur and patella with some spots on the retrolateral surface.

Morphology: Measurements a of a male specimen (MACN-Ar) and female specimen (MACN-Ar) in Table 2. *Prosoma*: Chelicerae with two subdistal teeth in the movable finger; anterior edge of the carapace with a median bulge and six setae, two on each side and two in the middle; tegument densely granular in males, finely granular in females; anterior and posterior longitudinal sulcus, lateral sulcus and postocular furrow deeply marked; ocular tubercle medially situated on the carapace with a slight interocular sulcus, median ocelli one diameter apart. *Sternum*: Sternum type 2 (Soleglad & Fet 2003), much wider than long; apex width equal to posterior width; posterior emargination quite well developed, with convexed lateral lobes conspicuously separated. *Mesosoma*: Tergites I–VI smooth near the anterior margin and finely granular near the posterior margin; VII smooth medially, the rest densely granular, with two posterolateral carinae. *Metasoma*: segment I: ventral surface smooth, lateral surface with scattered granulation, dorsally smooth, dorsosubmedian, dorsolateral and median lateral carinae extend the entire length of the segment; segments II and III similar to segment I but less granular, with less well developed carinae and with four pairs of ventral setae; segment IV: dorsally smooth, lateral surfaces slightly granular, ventrally smooth with a large number of scattered setae; segment V: ventral surface smooth near the front margin and irregularly granular in the second half; the ventrolateral carinae extend throughout the entire length of the segment, but there is not a ventromedian carina (Fig. 52); the ventral setae usually comprise 5 rows: 1 basal row of 3–5 setae, 1 subbasal row of 2–4 setae, and 3 posterior rows of 1 or 2 setae; dorsal and lateral surfaces finely granular or smooth; in males the caudal glands occupy 15–20% of the dorsal surface (Fig. 51). *Telson*: Sparsely granular; vesicle with rounded ventral surface; aculeus slightly curved, of the same length as the vesicle (Figs. 54 & 55); the holotype of this species has a very conspicuous depression on the ventral surface of the telson (Cekalovic 1975, fig. 9), but it was not present in any of the specimens studied. The telson gland is divided into two separated halves (Fig. 53), but it is absent in almost 80% of the specimens. *Pedipalps*: Trichobothrial pattern, neobothriotaxic major type C: femur with 3 trichobothria: 1 *d,* 1 *i* and 1 *e*; patella with 3 ventral trichobothria, 2 dorsal trichobothria, 1 internal trichobothrium, and 13 external trichobothria: 3 *et,* 1 *est,* 2 *em,* 2 *esb* and 5 *eb*; chela with 27 trichobothria: 1 *Est,* 5 *Et,* 5 *v,* 1 *Esb,* 3 *Eb,* 1 *Dt,* 1 *Db,* 1 *et,* 1 *est,* 1 *esb,* 1 *eb,* 1 *dt,* 1 *dst,* 1 *dsb,* 1 *db,* 1 *ib,* 1 *it*; no intraspecific variation has been observed in these characters. Femur smooth, ventrointernal and dorsointernal carinae poorly developed, patella scarcely granular and without carinae; chela stout, with smooth tegument and a very developed ventroexternal carina (Figs. 56 & 57); in males the prolateral apophysis is well developed; movable finger with a central row of granules and 8–10 internal and external granules. *Legs*: Finely granular; telotarsi I and II with the inner ungue 5–10% shorter than the external. *Hemispermatophore*: Distal lamina thick and shorter than the basal portion (Figs. 48 & 49); cylindrical apophysis well developed, and longer than the laminar apophysis; basal triangle very well developed formed by three or four crests (Fig. 50); internal spines absent; basal spines well developed; row of spines well developed; distal crest undulated.

Variation.—Total length in males, 50–66 mm (n = 7; mean = 56.7), 55–68 mm in females (n = 7; mean 61.9). Pectines with 32–38 pectinal teeth in males (n = 9; median = 33), 30–33 in females (n = 10; median = 31).

Length/width ratio of the fifth metasomal segment 1.74–2.00 in males and females (n = 14; mean = 1.87). Length/height ratio of the pedipalpal chela 2.64–2.96 in males (n = 8; mean = 2.84), 2.96–3.13 in females (n = 8; mean = 3.03). Telotarsus I with 1–4 ventrointernal setae (n = 12; median = 2), 0 or 1 ventroexternal setae (n = 12; median = 0) and 6–9 dorsal setae (n = 12; median = 8). Telotarsus II with 4 or 5 ventrointernal setae (n = 12; median = 4), 1–3 ventroexternal setae (n = 12; median = 2) and 7 to 10 dorsal setae (n = 12; median = 8). Telotarsus III with 5 to 7 ventrointernal setae (n = 20; median = 6), 3–5 ventroexternal setae (n = 12; median = 4) and 9–11 dorsal setae (n = 20; median = 10). Telotarsus IV with 4–6 ventrointernal setae (n = 12; median = 5), 2–5 ventroexternal setae (n = 12; median = 4) and 5 or 6 dorsal setae (n = 12; median = 5). Fourth metasomal segment with 27–33 ventral setae (n = 8; median = 28). Fifth metasomal segment with 8–10 ventrolateral setae (n = 20; median = 9); and 8–10 lateral setae (n = 20; median = 8).

Distribution.—*Brachistosternus* (*L.*) *negrei* is the southernmost species of the genus in Chile. It has been collected in southern Chile, in Maule and Bio Bio provinces (Fig. 58).

Material examined.—CHILE: *Maule province*: Curico, Los Queñes (35°10′S, 70°47′60″W), 4 ♀ and 9 juveniles, 1 January 1984, Roig Alsina (ARA); 2 ♀, 3 juveniles and 1 ♂, Maury (MACN-Ar); Vilches (35°36′S, 71°12′W), 1 ♀, 7 January 1989, Maury (MACN-Ar); Curico, Las Tablas (34°58′60″S, 71°13′60″W), 2 ♀, 3 ♂ and 2 juveniles, 10–15 February 1985, Peña (AMNH); Maule, Cuyarranquil (west Cauquenes) (35°58′S, 72°20′60″W), 2 ♂, 1 ♀ and 2 juveniles, 24–31 January 1981, Peña (AMNH); Tonlemo, Talca (35°7′S, 72°20′60″W), 1 juvenile, 14–21 December 1984, Peña (AMNH); Linares, Bullileo (35°51′S, 71°35′60″W), 2 juveniles, 13 January 1979, Peña (AMNH). *Bio Bio Province*: Ñuble, Chillan (36°36′S, 72°7′W), 3 ♂ and 2 ♀, January 1970, Peña (AMNH); Ñuble, 8 km west San Fabián de Alico (36°32′60″S, 71°32′60″W), 1 ♂, 1 ♀ and 2 juveniles, 19 January 1985, Platnick & Francke (AMNH); 50 Km. west San Carlos (35°58′S,

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Figure 58.—Map with the distribution of the Chilean species of the genus *Brachistosternus*.

71°37′60″W), 1 ♂, 26 December 1950, Ross & Michelbacher (MZUC).

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SHORT COMMUNICATION

PREDATION BY *ARGYRODES TRIGONUM* ON *LINYPHIA TRIANGULARIS*, AN INVASIVE SHEET-WEB WEAVER IN COASTAL MAINE

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ABSTRACT. A female *Argyrodes trigonum* (Theridiidae) was observed feeding on a female *Linyphia triangularis* (Linyphiidae), a recently established European immigrant in Maine. Multiple observations of *Argyrodes* spiders inhabiting *L. triangularis* webs suggest that this invasive sheet-web weaver is not immune to web invasions, kleptoparasitism or predation by *A. trigonum*. The potential impacts of *A. trigonum* on the invasion dynamics of *L. triangularis* are unknown, but likely to be minimal.

Keywords: Kleptoparasitism, araneophagy, exotic

Members of the genus *Argyrodes* Simon 1864 (Theridiidae) are known for diverse and flexible foraging strategies. Although capable of spinning small tangle webs of their own, many species forage more often as kleptoparasites, web-stealers or predators of other spider species (Cangialosi 1991, 1997). *Argyrodes trigonum* (Hentz 1850) is common in the eastern U.S. (Exline & Levi 1962), and is also found in Ontario (Levi & Randolph 1975) and Québec (Paquin et al. 2001). Cangialosi (1997) provides a thorough description of the diverse and flexible foraging strategies of this species.

The European Hammock spider, *Linyphia triangularis* Clerck 1757 (Linyphiidae), has recently become established in parts of coastal Maine (Jennings et al. 2002) and apparently is spreading inland. In some coastal habitats, such as those of Schoodic Peninsula in Acadia National Park, the invasion has become severe, with population densities of *L. triangularis* reaching 12 individuals/m^2. In these high-density areas, native linyphiids, such as *Neriene radiata* (Walckenaer 1841) and *Pityohyphantes costatus* (Hentz 1850), are now scarce (Houser, Jakob, & Jennings, pers. obs.).

During the summer of 2002, while studying the invasion at Acadia N.P., we noticed *A. trigonum* in some webs of *L. triangularis*. On 24 August 2002, we observed an adult female *A. trigonum* feeding on an adult female *L. triangularis* in the prey's web. The predator-prey habitat was a roadside/coniferous forest-edge on the Schoodic Peninsula (Winter Harbor, Maine). The *L. triangularis* was not extensively digested, suggesting that the capture by *A. trigonum* was recent. Several more *A. trigonum* were found nearby in the superstructure of *L. triangularis* webs. To the best of our knowledge, the earliest observation of *Argyrodes* in the web of *L. triangularis* was on 28 August 1999, when D.T.J. collected a juvenile *Argyrodes* sp. from a female-occupied web of *L. triangularis* in Pittston, Kennebec County, Maine.

During August and September of 2003, surveys of *L. triangularis* webs were conducted at four locations in Maine to determine whether the occupation of *L. triangularis* webs by *A. trigonum* is a common occurrence or better described as a novelty. Surveys were conducted in habitat favorable to *L. triangularis*, primarily seedlings, saplings, shrubs and forbs. At two of the locations, the proportion of webs containing at least one *A. trigonum* was rather high: 11 out of 36, or 30.6% (Dixmont, Penobscot Co.), and 19 out of 35, or 54.3% (Garland, Penobscot Co.). At the other sites, however, the frequency of *A. trigonum* was low; none were found among 33 webs surveyed at Guilford, Pis-

cataquis Co., and only 1 was found among 11 webs at Milbridge, Washington County. Multiple *A. trigonum* (always 2 or 3) were found in 11 of the 115 (9.6%) webs surveyed, or 11 of the 31 (35.5%) webs containing at least one *A. trigonum*. Although not found in these surveys, higher levels of occupancy are possible. D.T.J. observed 5 or 6 *Argyrodes* juveniles co-inhabiting a female *L. triangularis* web in Garland, Penobscot County.

At two of our survey sites, the proportion of *L. triangularis* webs containing *A. trigonum* is comparable to, if not higher than previously observed rates of *A. trigonum* in other linyphiid webs. Overall, 27.0% of *L. triangularis* webs surveyed in 2003 contained *A. trigonum*. In a large study of the foraging strategies of *A. trigonum*, Cangialosi (1997) recorded *A. trigonum* co-inhabiting 6.1% of *N. radiata* webs, 1.9% of *P. costatus* webs and 2.6% of *Frontinella pyramitela* (Walckenaer 1841) webs. Our observed proportions may be high relative to those reported in Cangialosi (1997) due to a variety of factors, including differences in sampling method, date or location, and therefore should be interpreted cautiously.

Our observations support the already considerable evidence that foraging behavior of *A. trigonum* is very flexible. Species of *Argyrodes* have been classified as either host specialists, which use a variety of behavioral techniques to exploit their hosts, or host generalists, which have a more limited behavioral repertoire, but can take advantage of a large variety of hosts (Vollrath 1984; Whitehouse 1988). Cangialosi (1997) has argued that a host generalist would also benefit by having a variety of techniques at its disposal and presents *A. trigonum* as an example. The behavioral repertoire of *A. trigonum* is quite broad; in addition, hosts of *A. trigonum* include (in various geographic locations) linyphiids, agelenids, theridiids, and araneids (Larcher & Wise 1985; Cangialosi 1997). The ability of *A. trigonum* to exploit an introduced exotic species is further evidence that it is a host generalist, and that its foraging success is not, at least at present, likely to be driven by co-evolution with any particular host.

The possible effects of *A. trigonum* on the invasion of *L. triangularis* are unclear. Because *A. trigonum* makes use of both *L. triangularis* and native host webs, it could mitigate or exacerbate the effects of the invader on native populations. It would be useful to know the relative preference, if any, that *A. trigonum* has for native linyphiids *vs.* the invader. Host-web structure, particularly the amount of barrier silk, affects selection and occupancy potentials of *A. trigonum* (Cangialosi 1997). Superficially, the semi-dome shaped webs of *L. triangularis* are more similar to those of *N. radiata* and *P. costatus* than the bowl and doily webs of *F. pyramitela*. At the Schoodic study site, *N. radiata* and *P. costatus* appear to have declined more dramatically than *F. pyramitela*. However, in New Hampshire, Cangialosi (1997) found that *A. trigonum* uses *N. radiata* as hosts more often than either *F. pyramitela* or *P. costatus*. Comparable host-preference data including *L. triangularis* in addition to native hosts are needed to better evaluate the impacts, if any, of *A. trigonum* on this invasion. Because of its host-generalist behavior, we suspect that *A. trigonum* has (and will have) minimal regulatory impacts on populations of *L. triangularis* in Maine. Instead, assemblages of natural enemies (e.g., parasites, parasitoids, predators, and pathogens) may be needed for control or containment of this invasive spider.

The impetus for this note comes from the sharp eye of Adam Porter, who made the initial discovery and observation of the predation encounter on 24 August 2002. The 2003 surveys were conducted with the much appreciated assistance of Nancy Jennings and Frank Graham, Jr. We are grateful to David Manski, Chief Biologist, Acadia National Park, for issuance of collecting permits, and to Park Biologist Bruce Connery for logistical support. Voucher specimens are deposited in the park collection of the Acadia National Park Research Center, Bar Harbor, Maine.

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Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

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